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THE LIVING BIRD

THIRTEENTH ANNUAL....1974

Cornell Laboratory of Ornithology

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of the

Cornell Laboratory
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1974

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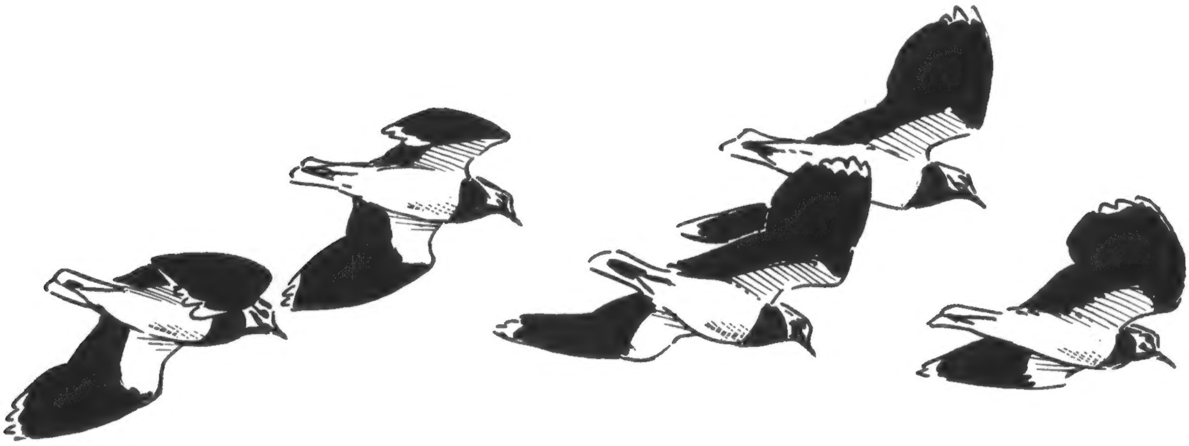

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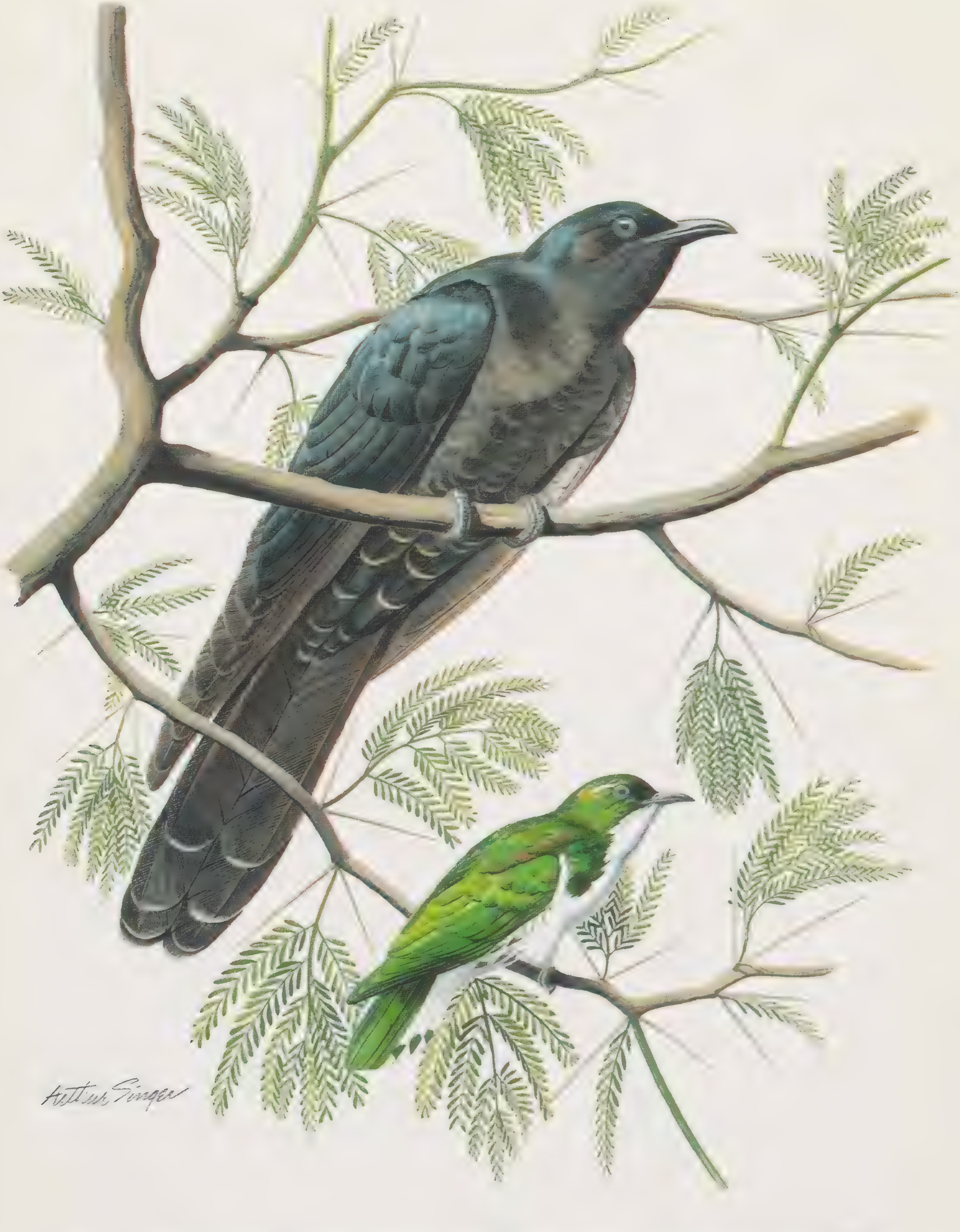

Plate I. Black Cuckoo (*Cuculus clamosus*) and Klaas's Cuckoo (*Chrysococcyx klaas*). Painting by Arthur Singer.

BREEDING BIOLOGY OF TWO CUCKOOS AND THEIR HOSTS IN SOUTH WEST AFRICA

R. A. C. JENSEN AND C. F. CLINNING

Photographs by the authors

Crude Fude[1]

When in thoughtful or in pensive mood
Upon brood parasites I brood,
I wonder why they choose such food
As hairy caterpillars, well choo'd.
Why don't they take them nood?

M. K. Rowan
October, 1971

Mood Rued

To take them nood
Would be too rood.
You see they fear that they'll be boo'd
If they indulge in things so lood.
How *can* you be so trooly crood?

Each parasite's a natch'ral killer
Of every sort of caterpillar.
So if a cuckoo likes the hair
That, surely, is his own affair!

C. J. Skead
November 1971

Since Friedmann's (1948) classical work on the African cuckoos, much new information has been accumulated, some of which Friedmann himself collated and published (1949, 1956, 1967, 1968). For cuckoos of southern zoogeographic Africa, the most recent published reviews attempting an up-to-date collation and synthesis of available data are those of Payne and

---

[1] This exchange of rhymes took place while M. K. Rowan and C. J. Skead were preparing manuscripts for a handbook on the cuckoos.

Payne (1967) and Jensen and Jensen (1969). The latter paper is used here as a point of departure.

In the course of broader studies in central South West Africa, opportunities arose to study the Black and Klaas's Cuckoos. Most of the data discussed in this paper formed part of a three-year study of bird breeding ecology in central South West Africa carried out by the senior author between 1968 and 1971. In the species accounts, only new facts and interpretations are emphasized, and the reader is referred for background material to Friedmann and others.

The Cuckoos

Black Cuckoo (*Cuculus clamosus*)

The Black Cuckoo is a typical member of its genus, measuring about 280 millimeters in length and weighing 70 grams. It occurs rather commonly in bushveld country in southern Africa as a summer migrant, and has a distinctive and penetrating advertising call, a hollow whistled *whoo, whoo-wheee.* Very little has been published about its breeding habits. The main hosts appear to be the *Laniarius* shrikes, but Jensen and Jensen (1969) could trace only 14 well-authenticated breeding records for southern Africa. The eggs were known from only two reasonably authentic nest-egg records, and a few oviduct specimens.

Klaas's Cuckoo (*Chrysococcyx klaas*)

Klaas's Cuckoo is the smallest of the African cuckoos, measuring about 180 mm and weighing about 30 gm. It belongs in the aptly named "glossy cuckoo" group, a genus with typical cuckoo habits, which differs from *Cuculus* in having well-marked sexual dichromatism. Klaas's Cuckoo occurs in a rather irregular pattern in southern Africa, usually in thicker bushveld and woodland regions. In some areas it appears to be at least partly resident. It has a distinctive whistled call, *whitjeh,* repeated in short bouts of calling from reasonably well-defined territories. A fairly large number of breeding records has been assembled from various parts of Africa showing that Klaas's Cuckoo parasitizes the nests of numerous small insectivorous birds. The eggs are not well known, due partly to confusion with the eggs of congeners in areas of sympatry. Friedmann (1968) records 59 hosts — some on very flimsy evidence — from the total range of this cuckoo. However, Jensen and Jensen (1969) accepted only 48 records from 14 "biological hosts" (hosts recorded as raising a cuckoo beyond hatching) in South Africa.

Methods and Study Areas

Methods

We investigated intensively study plots in five well-separated study areas with different habitats and climate (Figure 1). Ranges of territorial birds were roughly delineated, and we obtained as many breeding records as possible of all species. At Daan Viljoen Game Park, the junior author played the leading role in the general project during his period of residence there (1969 to 1970).

Data on breeding were entered on nest record cards of the Nature Conservation and Tourism Division in Windhoek and at the Percy FitzPatrick Institute in Cape Town. We made special efforts not to overlook eggs of parasitic birds.

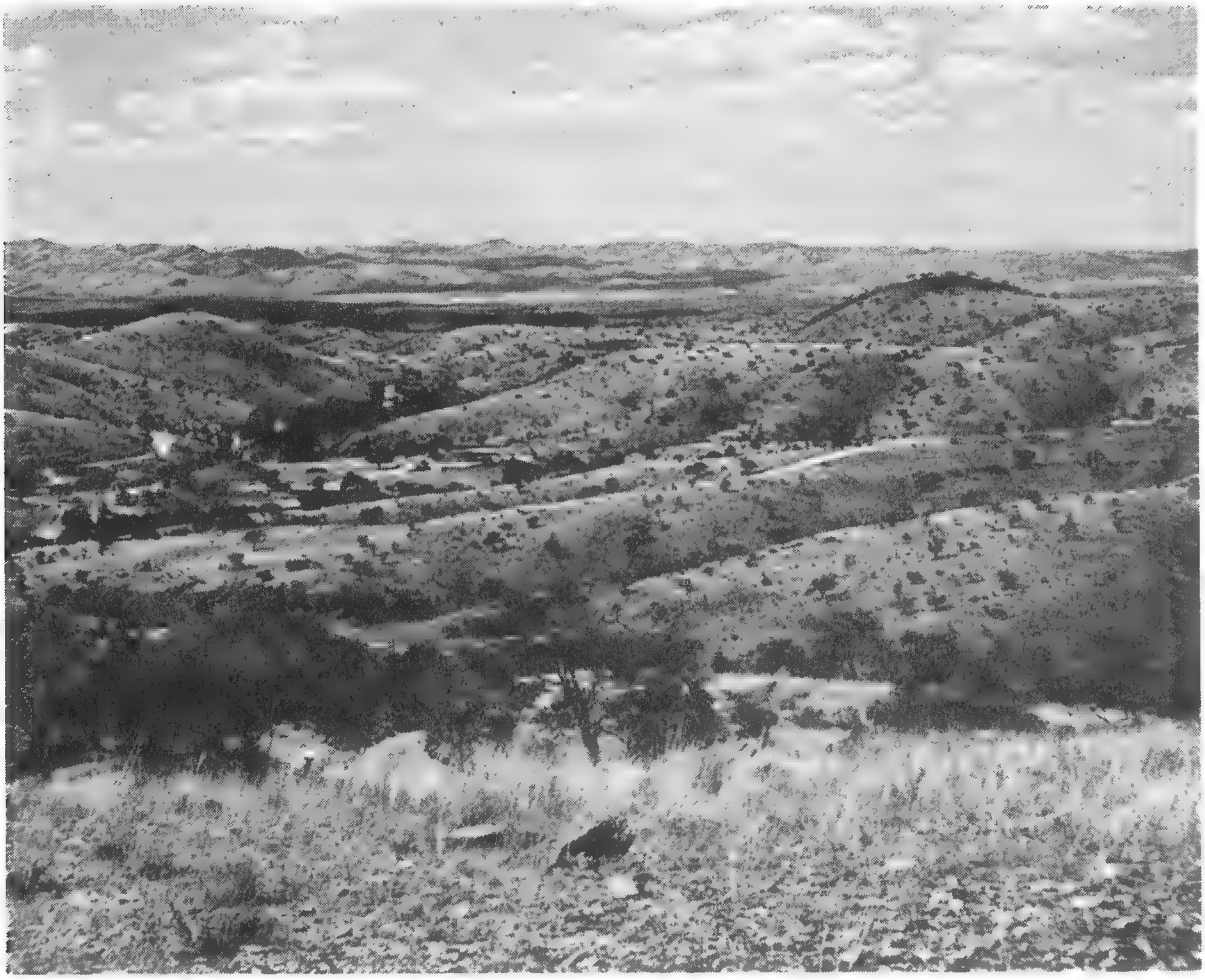

Figure 1. General view over Daan Viljoen Game Park looking east toward the rest camp and Windhoek. Cuckoos and hosts mostly frequent taller and denser trees and bushes in the valleys. Photographed in May 1971 after average rains.

Study Areas

The location, altitude, and rainfall of the five study areas may be seen from Figure 2. The nomenclature of plants listed follows Merxmüller (1966-1972).

The Black Cuckoo and its host species, the Crimson-breasted Shrike (*Laniarius atrococcineus*), occur commonly at Daan Viljoen Game Park near Windhoek (Figures 1 and 2), where they frequent the dry, but seasonally flooding, watercourses. These stream-beds support a denser and taller stand of trees than do the surrounding savanna-covered hills. Dominant trees in the valleys are, in descending order of approximate size: *Acacia giraffae* (to 10 meters), *A. karroo, Ziziphus mucronata, Rhus marlothii, A. mellifera detinens,* and *A. hebeclada* (3–5 m). In the lower eastern zone of the park, where a permanent dam-fed stream runs along the boundary, the gentle slopes are heavily scrub-encroached because of severe over-grazing prior to 1962 when it became a part of the park. In this area there are clumps of fair-sized (4–5 m) *Acacia reficiens* and *A. hebeclada* on the slopes, as well as *A. giraffae* (few), *A. tortilis heteracantha* (fewer), *A. mellifera* and *Albizia anthelmintica.* Shrikes and cuckoos frequent these slopes; in fact, the greatest concentrations of both are found in this scrubby area and along the adjacent stream. Further description and illustration may be found in Clinning and Jensen (1973).

Klaas's Cuckoo is uncommon to rare in South West Africa, known from less than ten records prior to 1968. Whether the vast subsequent increase in observations is due to an increase in its population, or to increased bird-watcher activity is hard to say, but the latter seems more likely. It is a shy, difficult-to-see species in South West Africa. We found it in all study areas, and breeding in four of them (Figure 2). It is rare at Daan Viljoen Park, but somewhat more common at "Djab," a farm at the foot of the escarpment, and also at Spitskoppe on the edge of the Namib Desert. It penetrates the mountainous northeastern sector of the Namib Desert Park regularly in years with good rainfall.

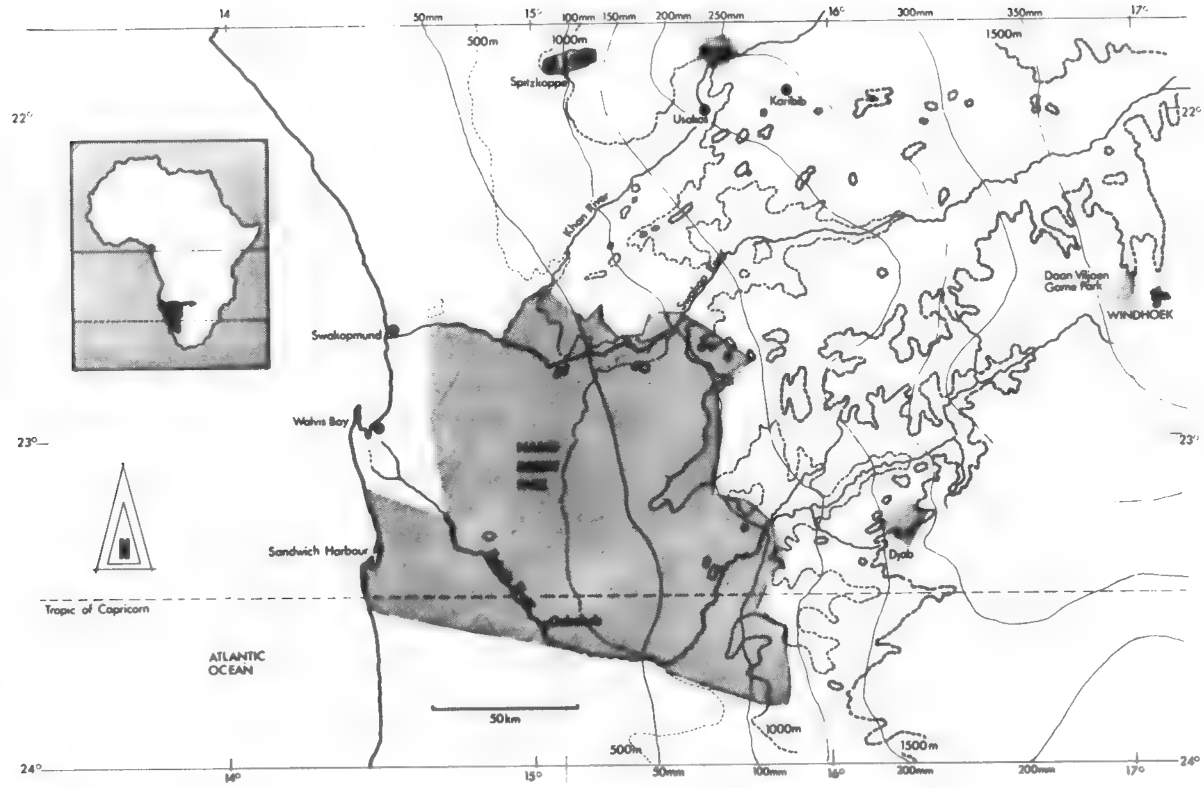

Figure 2. Map of central South West Africa showing study areas in relation to rainfall and altitude.

Klaas's Cuckoo locally prefers hilly areas with communities of acacia and *Commiphora* (paperback trees). Djab lies in mountainous terrain, with open bushveld (small-tree savanna) on the slopes and somewhat taller trees along the dry stream-beds of the valley bottoms. The grasses are predominantly annuals (by contrast with Daan Viljoen Park), perennial forms being confined to cliff bases and other relatively moist spots. On the slopes, dominant trees are *Acacia erubescens, A. mellifera, Albizia anthelmintica, Boscia albitrunca* and, rarely, nearly pure stands of *Aloe dichotoma*. In the valleys, a few *Acacia karroo, A. giraffae, Euclea pseudebenus,* and *Ziziphus mucronata* from four to seven meters high occur at intervals. Flowering shrubs and flowering annual herbs are more in evidence than at Daan Viljoen Park, and hence Dusky Sunbirds (*Nectarinia fusca*) are fairly common.

The Spitskoppe (spelled variously on maps as Spitzkoppe, Spitzkuppen, Spitzkopjes, etc.) is an isolated hill complex consisting of two major granite outcrops in the relatively flat plain on the edge of the Namib (Figure 3). Groot Spitskop (Gross-Spitzkuppe, -koppe, -kopje, etc.) rises in spectacular bare "kops" or bosses, up to 600 meters above the surrounding plains. Imemdiately to the east, a series of smaller kops form the adjoining Pontok Mountains. Klein Spitskop lies 10 kilometers to the west, and has a less abrupt aspect, hence more vegetation on the slopes, although it receives probably only 90–100 mm average rainfall compared to 12 mm or so at Groot Spitskop. Due to runoff effect, the plains at the base of the hills support an area of denser vegetation than the plain proper. *Acacia reficiens, A. hebeclada, A. tortilis, A. senegal* var. *rostrata,* and *A. giraffae* (2–7 m) are all common in this community, along with smaller trees and bushes such as *Boscia foetida, Salvadora persica, Cordia gharaf, Terminalia prunioides,* and others. The kops themselves do not have acacias, but *Commiphora virgata, C. tenuipetiolata, C. glaucescens, Sterculia africanna,* and *Aloe dichotoma* (Groot Spitskop only) are dominant tree forms while bulbous-trunked *Moringa ovalifolia* and *Cyphostemma currorii* and the cactus-like *Euphorbia virosa* are also prominent in places. "Bushman's Paradise" plateau in the Pontok Mountains has a rich mixture of slope and base vegetation, a feature of which is the profusion of flowering shrubs that in summer, autumn, and early winter attract a large population of Dusky Sunbirds.

The north-eastern mountain sector of the Namib Desert Park (Figure 4) might be described as a mixture of a drier version of the Djab escarpment biotope and the Klein Spitskop biotope. The rainfall is probably much the same as at Klein Spitskop (there are no exact figures), but the vegetation is more diverse, partly beacuse the basic, rugged schist formations show numerous granitic intrusions. Thus the slopes are covered basically, but variably, with an open *Commiphora-Acacia* flowering shrubs community, and the dry streams and valley bottoms support larger *Acacia reficiens* (to 4 m), *A. tortilis* (to 8 m), *A. giraffae* (to 8 m), *Euclea pseudebenus*, and even scattered specimens of two *Ficus* species, among others. There are few perennial grasses.

THE BLACK CUCKOO AND ITS HOST

Crimson-breasted Shrike Breeding Biology

In South West Africa the only known host of the Black Cuckoo is the Crimson-breasted Shrike, measuring 230 mm and weighing 50 gm. Hoesch and Niethammer (1940) had no definite nest parasitism records of Black Cuckoos. The first definite record of the Black Cuckoo with this host seems to be from nest record cards of E. Davison, who found a half-grown nestling at Wankie, Rhodesia in January 1958. M. K. Rowan *et al.* (1964) recorded the first definite record of this host-parasite combination from South West Africa — a fledgling being fed by Crimson-breasted Shrikes near Windhoek in February 1964.

A cuckoo's breeding biology can be understood only in the context of its host's breeding cycle. An excellent study of Crimson-breasted Shrike breeding biology in the Transvaal was recently published by Tarboton (1971), and we will refer to relevant items that confirm and/or add to his findings in the context of our own study.

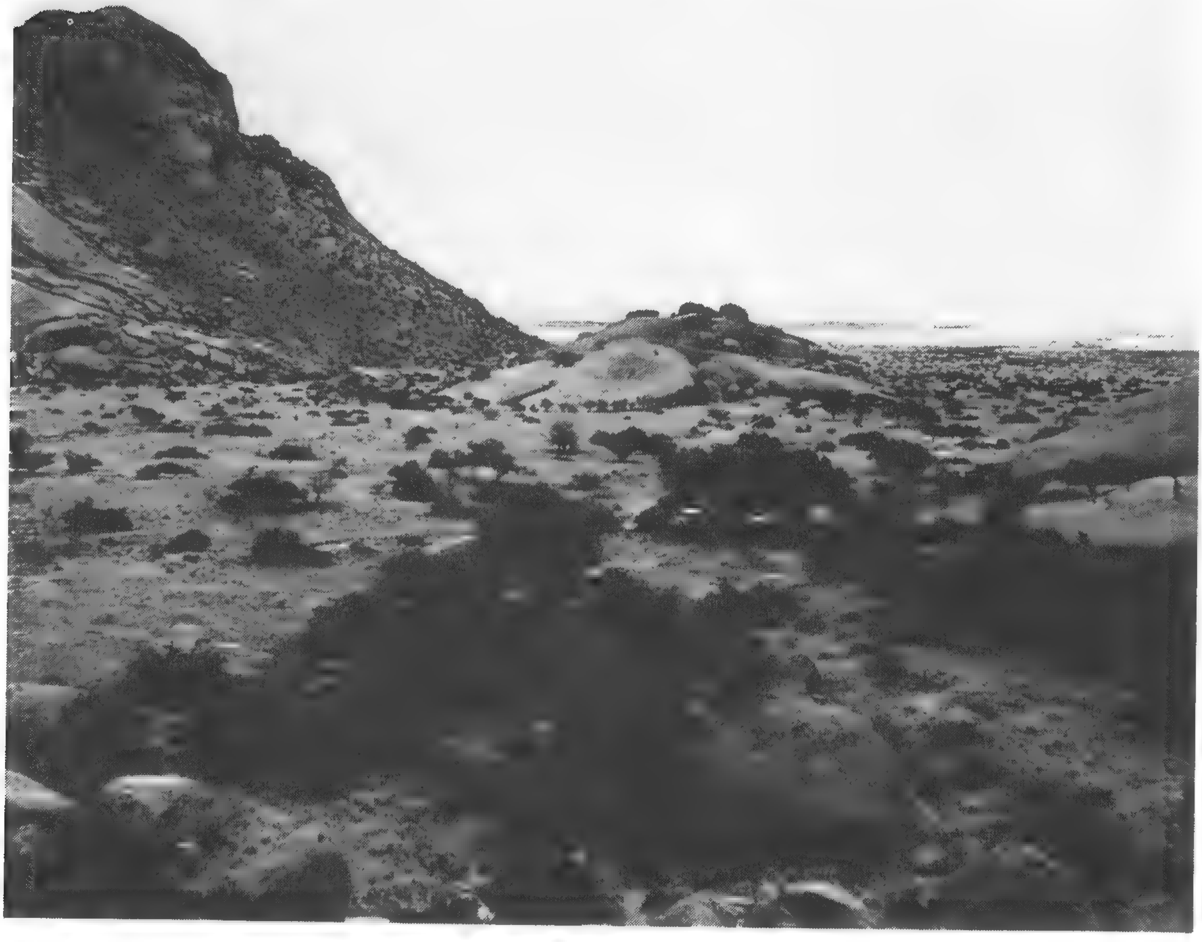

Figure 3. Groot Spitskop, West Camp study plot at the height of summer rains in an average year. Largest trees are *Acacia giraffae*. March 1971.

The Crimson-breasted Shrike occurs widely in thornbush country where the annual rainfall exceeds 200 mm in South West Africa. It is insectivorous, resident, and breeds mostly during the warmer months when insect food becomes plentiful. Tarboton (1971) found pairs occupying territories about 4.5 hectares in size during the summer, and we broadly confirmed his findings regarding territoriality. An exasperating characteristic of the species is its readiness to desert its nest at the slightest provocation (Tarboton, 1971; and pers. observ.). This tendency, coupled with the generally high predation rate in Africa (Rowan, 1969; Rowan and Broekhuysen, 1962) hampered efforts to follow nests through the complete cycle.

Over four years, pairs of shrikes occupied more or less fixed territories, at least in summer. None was marked, but one pair was characterized by a very rare white egg morph, and other pairs had subtle behavioral characteristics by which they were recognized.

The shrikes build cup nests (Figure 5) of bark strips and rootlets, well concealed in trees, mostly acacias of one or two preferred species. Two or three eggs form the clutch. At least two broods can be raised in a good season and renesting occurs readily in cases of nest loss (Tarboton, 1971; and nest record cards). Table 2 shows an interesting example of one pair's multiple nesting efforts at Avis Dam, near Windhoek, in the exceptionally rainy 1973-1974 season.

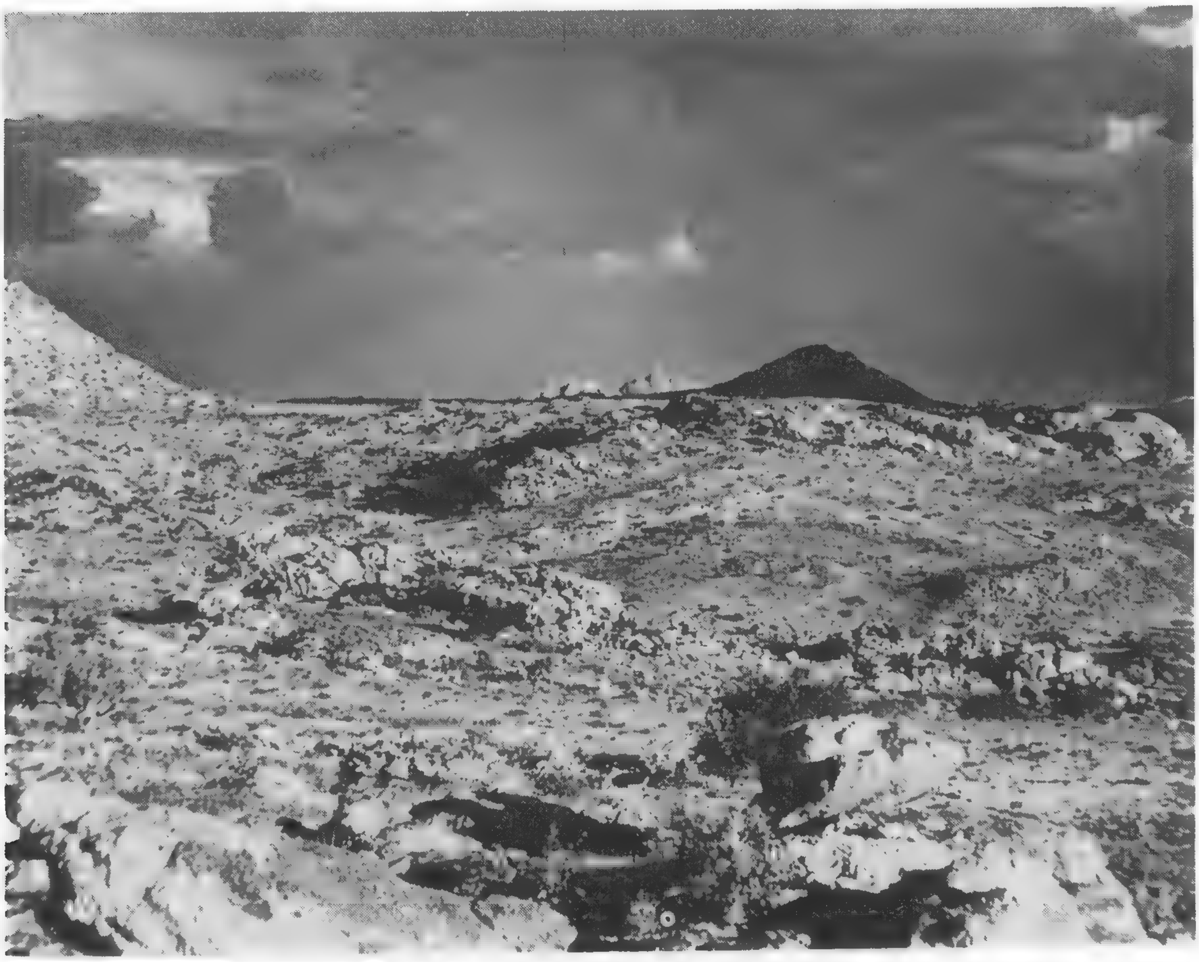

Figure 4. North-eastern corner of the Namib Desert Park, looking east toward the border. Klaas's Cuckoos and hosts frequent this sparsely vegetated broken country. Photographed after good rains in April 1972.

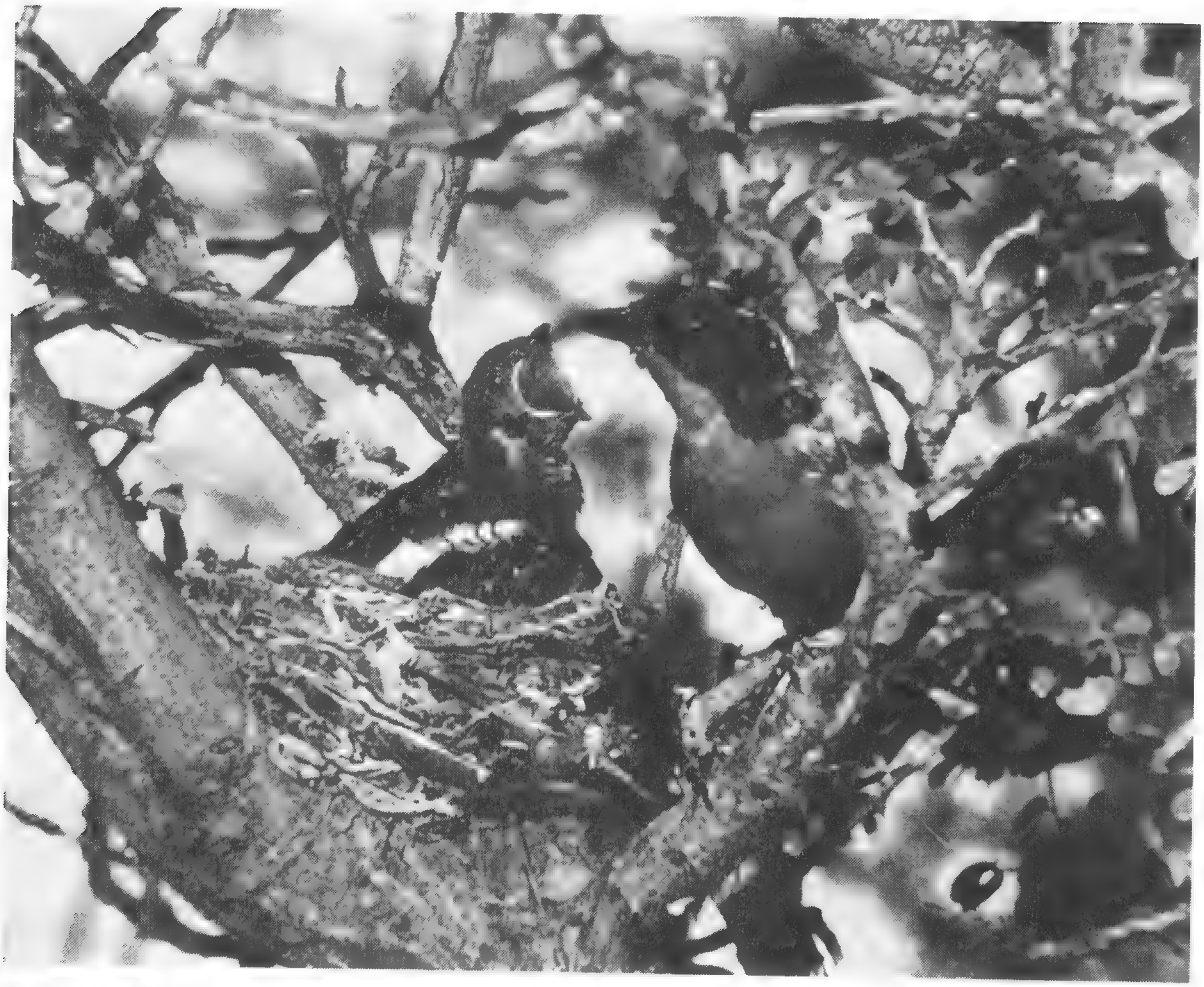

Figure 5. Female Crimson-breasted Shrike (*Laniarius atrococcineus*) with 17-day nestling shrike. Avis Dam, Windhoek, 7 May 1974.

The eggs are whitish, often color-tinged, and heavily marked with brownish and grayish concentrated at the thick end (See Plate II, Figure 6, and Table 3.). A rare pure white morph exists. Measurements from central South West Africa range from 22.9 to 24.8 mm × 17.2 to 18.2 mm (17 authenticated eggs).

Incubation takes about 16 days (Tarboton, 1971; and nest record cards), usually beginning with the second or third egg, but Tarboton (1971) recorded some birds incubating from the first egg. The nestling progresses from a naked, purplish hatchling through the pin-feather stage at about six days to a fully feathered, but short-tailed, fledgling at about 19 days. Fledglings utter a mewing peep, but are rather quiet and unobtrusive by comparison with some shrikes. Plumage changes may be used as aging criteria up to independence at about 35 days (Tarboton, 1971). Tarboton records one instance of a second clutch being initiated when the single young of the first brood was only 11 to 12 days out of the nest.

Breeding season information on the Crimson-breasted Shrike in South West Africa appears in Table 1, based on nest record cards and the literature. From these records, it is clear that almost all nesting occurs in the warmer months from October to March. The rains, however, do not normally start until November or December (earliest in the north-east, latest in the west and south-west). Our detailed records relating to climate, insect abundance, and nesting in Daan Viljoen Game Park from 1968 to 1971

TABLE 1

Egg Dates[1] of Black Cuckoo and Crimson-breasted Shrike in South West Africa

Month		*1969–1970*		*1970–1971*		*1971–1972*		*Total*[2]	
		Parasite	*Host*	*Parasite*	*Host*	*Parasite*	*Host*	*Parasite*	*Host*
October	1–15	—	—	—	—	—	1(DV)	0	3
	16–31	—	—	—	—	—	—	0	0
November	1–15	—	—	—	1(DV)	—	—	0	2
	16–30	—	—	—	—	—	—	1	4
December	1–15	—	1(DV)[3]	—	—	—	—	0	3
	16–31	—	—	—	—	—	—	0	1
January	1–15	—	1(DV)	—	1(DV)	—	1(DV)	1	5
	16–31	—	—	—	1(DV)	—	2(DV)	1	4
February	1–14	2(DV)	2(DV)	1(DV)	1(DV) 1(A)[4]	2(DV)	1(DV)	5	5
	15–28	2(DV)	2(DV)	1(DV)	2(DV)	—	1(DV)	4	6
March	1–15	—	—	1(DV)	2(DV)	—	—	2	5
	16–31	—	1(DV)	2(DV)	2(DV) 2(A)	—	—	2	5
April	1–15	—	—	—	—	—	—	0	1

[1] Calculated or estimated to half-month in which cuckoo egg and last egg of host clutch, respectively, were laid, including oviduct eggs. One additional egg date in July, *in* Hoesch and Niethammer (1940).

[2] Including all egg dates from authenticated South West African records.

[3] DV = Daan Viljoen Game Park.

[4] A = Ameib.

TABLE 2

Multiple Renesting of Crimson-breasted Shrike Pair[1] at Avis Dam 1973–1974

Estimated or known egg date	*Last seen*[2]	*Fate, remarks*
21 November	20 February	Two shrike fledglings first found on 19 January, when about 30 days out of nest, self-feeding. Still one with parents on 20 February.
27 January	21 February	Three shrike eggs, one supplanted by Black Cuckoo egg. 11-day cuckoo rescued, hand-raised from 21 February (see text).
4 April	10 May	Found 21 April with single shrike chick about one day old. Fledged about 9 May.

[1] Female recognized by voice, characteristic scruffy appearance, and remarkable tameness. Male not definitely identifiable as the same individual throughout.

[2] Last date on which brood was seen with parents.

(Jensen and Clinning, unpubl. ms) show that the shrikes begin nesting with the onset of rising temperatures and the concomitant increase in insect food, provided the previous season was a good one (carry-over effect, see page 000).

Breeding Biology of the Black Cuckoo

The Black Cuckoo arrives later in central South West Africa than in the eastern parts of South Africa (Friedmann, 1948; Skead, 1951). Its arrival depends on the rains. Although the bird is easily overlooked when silent, our records suggest that it appears in November if, and when, at least 50 mm of rainfall have accumulated in the new season. Hoesch and Niethammer (1940), among others, have commented on the association of its calling with rainy weather.

Black Cuckoos appear to follow the general *Cuculus* pattern, so well described by Chance (1940), in respect to territory, courtship, egg-laying, and other aspects of reproduction. Specific data are rather meager, however (Friedmann, 1948, 1956; Hoesch and Niethammer, 1940; Jensen and Jensen, 1969; Payne, 1971; Skead, 1951). Males call in fixed territories that may shift slightly from year to year, probably due to local environmental and host fluctuations. Females apparently come to the males for copulation, but their territorial relationships are unknown. Trios are not infrequently seen, probably two males and one female. Friedmann (1948) and Payne (1971) proved such associations in both this species and the Red-chested Cuckoo (*Cuculus solitarius*) by collecting some examples. Occasionally, we encountered larger groups, although Andersson (1872) was possibly exaggerating when he wrote about "... a flock of fully a dozen of these Cuckoos, creating a desperate hubbub on the 21st of December ..." In group situations, the cuckoos — apparently both sexes (Skead, 1951; Rowan, pers. commun.) — give a churring crescendo probably partly analogous to similar "bubbling" calls in other *Cuculus* species (Chance, 1940; Friedmann, 1948).

Calling continues till March, but is closely linked to weather and, presumably, host breeding. We have seen silent adults in early April, well after the last advertising calls; but they probably start moving north in stages as soon as the laying season ends (Table 1). The winter quarters are unknown.

Breeding Records

On 24 February 1970, we found a Black Cuckoo nestling in the pin-feather ("porcupine") stage in a Crimson-breasted Shrike nest in the lower area of Daan Viljoen Game Park. On 6 March, we found another shrike nest with four eggs. Two were larger and slightly but definitely different in color and markings from the other two (Plate IIa and Table 3). We watched this nest closely until two cuckoos hatched from the larger eggs. Both were kept alive for several days by alternately interchanging them between the nest and Clinning's home to ensure at least a 50 percent natural diet.

The cuckoo nestlings ejected both host eggs in typical *Cuculus* fashion by the third day after Chick No. 1 hatched. The larger cuckoo chick was removed by Jensen when six days old for chromosome studies and hand-rearing, but unfortunately died three days later. The second nestling fell prey to baboons when fourteen days old, by which time it could not be mistaken for any other cuckoo species (several occur at Daan Viljoen Park). These, then, were the first proven eggs of the Black Cuckoo and confirmed the status of the Crimson-breasted Shrike as a regular host in South West Africa.

A number of other parasitized shrike nests were subsequently found at Daan Viljoen Park, as well as one at Avis Dam, near Windhoek. Table 3 lists all records involving eggs; four other nest record cards from Daan Viljoen refer to nestlings and fledglings. Although a few of the eggs were not authenticated, their identity was virtually certain, since they conformed to the established criteria for Black Cuckoo eggs in their locale, as discussed later.

In 1974 two parasitized nests could be followed closely and yielded such a considerable body of information that they are described in some detail below:

Nest CC74–1B was at Avis Dam near Windhoek (see also Table 2). The shrike pair was found building (nest half complete) on 19 January. Two young of a previous brood, independent and about 30 days out of the nest, accompanied the adults. Nest visits were made as follows:

22 January, 18:30 — Nest looked complete, empty.

25 January, p.m. — One egg. One juvenile with adults, chased by them.

26 January, 18:45 — Two eggs, similar in size and markings.

27 January, 08:30 — Female (identified by voice; see Tarboton, 1971) sitting on two eggs, but one of these was different, a cuckoo's egg.

13:00 — Female relieved by male; nest now contained three eggs, the addition another shrike egg (Figure 6 and Table 2). The female was extremely bold, hopping around within one or two meters of an observer at the nest.

7–8 February — Assistants (R. Nöller and M. D'Alton), who took over observations, reported no change.

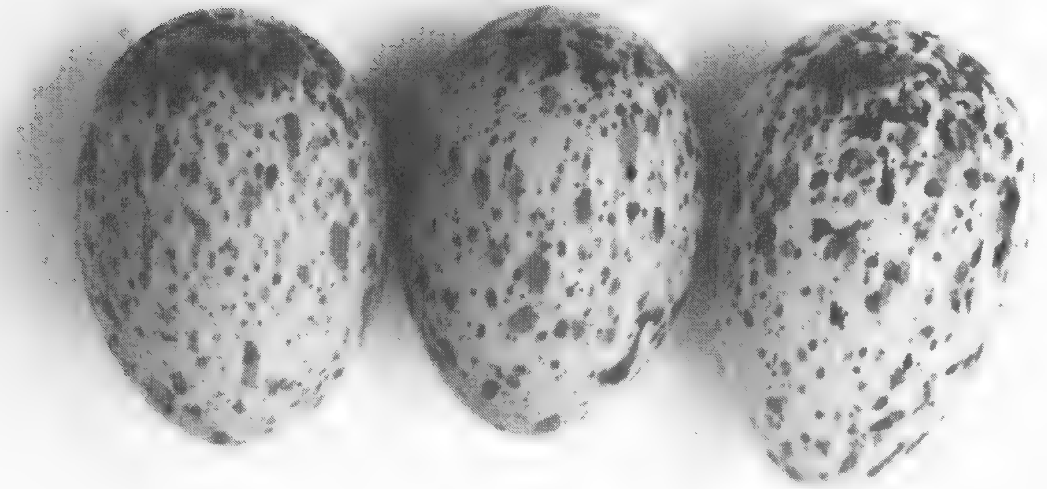

Figure 6. Parasitized clutch of the Crimson-breasted Shrike from Avis Dam. The egg on the right proved to be a Black Cuckoo's on hatching. January 1974.

9 February, 11:30 — Still three eggs (Nöller). *18:00* — Cuckoo nestling, newly hatched, pinkish olive, and the two smaller (shrike) eggs (D'Alton).

10 February, 09:00 — Two eggs still with cuckoo (D'Alton). *18:00* — Eggs out of nest, one on rim ignored by brooding shrike (D'Alton and Nöller).

16 February, 18:15 — Cuckoo nestling in early pin-feather stage, eyes open, typical pink mouth, pale flesh legs (Figure 7b). Excreted nauseous fluid, but no gape-lunge threat.

20 February, 07:30 — Heavy rains past few days. Nest collapsed, chick on ground, cold, wet, near death. Nestling revived, nest repaired and glued back in place.

Although the parents returned in the afternoon and showed some interest in the nest, they refused to brood, and fed the nestling only sporadically. By the following evening, it became clear that the 12-day-old nestling had been abandoned, and it was taken home and hand-raised. Kept in an artificial nest, the young cuckoo adapted quickly to its somewhat modified environment. It took its first flight at 20½ days of age (Figure 7e). Hereafter, it began to produce unencapsulated feces, and over the next week developed its persistent begging squeak. When 25 days old, it made its first attempts to handle a caterpillar in typical cuckoo fashion — passing it rapidly through the bill, beating it against a perch until the gut flew out and hairs, if any, mostly removed. These actions are similar to those described for American cuckoos (Bent, 1940). At first, however, it was exceedingly clumsy, frequently overshooting the caterpillar's ends, dropping it, winding it tightly around its bill, or even slapping itself in the eye with the gut or prickly hairs with visibly uncomfortable consequences. It also frequently "burned" itself by swallowing excessively "hot" caterpillars — those from which it had failed to remove sufficient hairs.

On 11 March, when 30 days old (10 days out of the nest), we banded this cuckoo and took it to its original nest area for release and "rehabitation." (We propose this term for use in this context, i.e., a return of hand-

TABLE 3

Description of the Eggs of the Black Cuckoo and its Host, the Crimson-breasted Shrike From Daan Viljoen Game Park and Avis Dam

Nest	*Shrike*[1]		*Cuckoo*[1]		*Authenticity and fate of eggs*
	Egg measurements[2]	*Egg description*	*Egg measurements*	*Egg description*	
CC70–1	23.3 × 16.9 23.3 × 17.6	White, blotched and speckled light, medium, and dark brown, concentrated at thick end.	24.2 × 17.9 23.6 × 17.7	Green-tinged white, marked as host but less red in markings, speckling finer, few blotches only at thick pole (one egg).	Proved; hatched, grew to 9 and 14 days.
CC71–1	23.7 × 17.5	Pinkish white, speckled light and dark brown, concentrated in ring at thick end.	25.9 × 18.2 More pointed.	White, speckled as host's, but slightly more heavily marked, especially at thick end, and more dark brown marking.	Unproved; nest perished.
UN–2	23.4 × 18.1 23.4 × 18.2	Faintly greenish white, heavily speckled and blotched pale reddish brown and dark brown, concentrated in ring at thick end.	24.3 × 18.3 Blunter small end.	White, heavily speckled as host's, but no large blotches.	Unproved; suspect egg disappeared, 2 shrikes hatched.
CC71–2	22.9 × 17.4 23.8 × 17.4	White, speckled and blotched medium, red-brown and dark brown, concentrated in ring at thick end.	27.3 × 19.1	Almost identical to host's in colors, but less red-brown in speckles, ring at thick end less dense.	Proved; ¾-term cuckoo, ½-term shrike embryos.
CC72	23.3 × 17.2 23.2 × 17.3	White with red-brown, pale brown, and dark brown speckles and small blotches, concentrated in ring at thick end. One pinker (fresher?).	24.6 × 18.3 25.6 × 17.5	More finely and evenly speckled than host's, concentrated at thick end but ring less dense.	Proved; one 4-day nestling cuckoo.

TABLE 3 (*Continued*)

Description of the Eggs of the Black Cuckoo and its Host, the Crimson-breasted Shrike From Daan Viljoen Game Park and Avis Dam

	Shrike[1]		*Cuckoo*[1]		
Nest	*Egg measurements*[2]	*Egg description*	*Egg measurements*	*Egg description*	*Authenticity and fate of eggs*
CC74–1B	24.1 × 17.9 23.8 × 17.4 More pointed.	White, green-tinged, one egg slightly pinker; profuse light and medium brown speckling, larger and more concentrated in ring at thick end. A few underlying mauve marks in ring.	26.2 × 18.1 Elongate, blunt.	Identical to host's in colors, but markings fractionally more discrete, greater proportion in darker shades.	Proved; hand-raised, rehabitated.
CC74–2	23.7 × 17.2 23.7 × 17.2 23.6 × 17.3	Whitish, speckled light and medium reddish brown, concentrated at thick end in vague ring, where some darker brown also. One egg whiter, less speckled. Some blotches, markings more discrete, darker, more red-browns, ring more defined.	24.3 × 17.8 Blunter small end.	Pale green-tinged white, markings exactly as host's, but more blotchy and generally paler brown.	Proved; 2 egg by chromosomes, egg-white; cuckoo hatched, fledged.

[1] Daan Viljoen Game Park and Avis Dam (CC74–1B).

[2] In millimeters.

raised or otherwise temporarily "borrowed" wild animals to the natural habitat. "Rehabilitation" appears to us to have erroneous and/or undesirable connotations in this usage.) At this stage (Figure 7f) it could process its own food (still rather clumsily) but could rarely be persuaded to pick it up off the substrate, preferring to squeak loudly for hours in nerve-racking fashion. We visited the cuckoo twice a day for feeding and observed it for a total of some five hours. It very rapidly adapted to its new environment and developed some associations with birds in the area. Because of its behavior, we suspected that it occasionally received food from some of these birds, and possibly from adult Black Cuckoos still frequenting the area; but we saw no actual instances of feeding by either the original foster-parent shrikes or any other birds.

At the time, hairy caterpillars of the Eupterotid moth (*Trichophiala devylderi*) were still abundant on the acacias at Avis Dam. On 13 March we observed the young cuckoo taking and successfully processing two of these, although it still came hungrily to its human foster-parent when called. When we next visited the area on 20 March, we found it in the same general one-hectare area in excellent condition and no longer begging. On the following day, when 40 days old, we persuaded it to come down for food only with difficulty; conflcting impulses to flee and to respond to the old feeding rountine were very evident. We observed for about two hours, during which the cuckoo fed expertly in between long bouts of preening, sunbathing, and sitting watchfully.

Growth stages of this bird from 7 to 30 days are shown in Figures 7b to 7f. Chromosomal analysis showed it to be a female.

One nest (CC74–2) was found with four eggs at Daan Viljoen Park on 2 March 1974. Two of these were identical in size and color, typical of Crimson-breasted Shrike eggs in the area. One of the remaining eggs was a typical Black Cuckoo egg. The fourth egg was different from the others, being whiter and differently marked (see Table 3 and Plate II). We suspected this egg came from a second female cuckoo, but chromosomal analysis of this embryo and one from the typical shrike egg revealed them both to be shrikes. This was confirmed by egg-white protein electrophoresis, which showed, furthermore, that the same female laid both eggs (C. G. Sibley, pers. commun.). Together with another similar case, this underlined the ease with which even a well-attuned, discriminating eye may be fooled.

Subsequent history of this nest was as follows:

13 March, 11:45 — Two eggs, no sign of pipping.

14 March, 09:45 — No change.

15 March, 09:15 — Cuckoo egg pipped. *10:30* — Cuckoo nestling out, no egg shell remains in nest (Figure 7a). Pinkish olive skin, pink feet. Gape and mouth dull olive-pink. Begged with mouth directed vertically. Other egg showed no sign of hatching.

30 March, 17:00 — Nestling (15 days old) alone in nest. Banded.

5 April, 09:30 — Cuckoo (21 days old) sitting motionless and well hidden in twigs 1.5 meters above nest (Figure 7e).

6 April, 08:15 — Cuckoo in the top of a tree 50 m from nest tree. Flew adequately, but, when disturbed, crash-landed in the next tree. Mostly silent, but after two hours began to squeak very softly, virtually inaudible from six meters. Shrikes stayed away. The cuckoo was not found on 9 April, although we observed the shrike pair in the area.

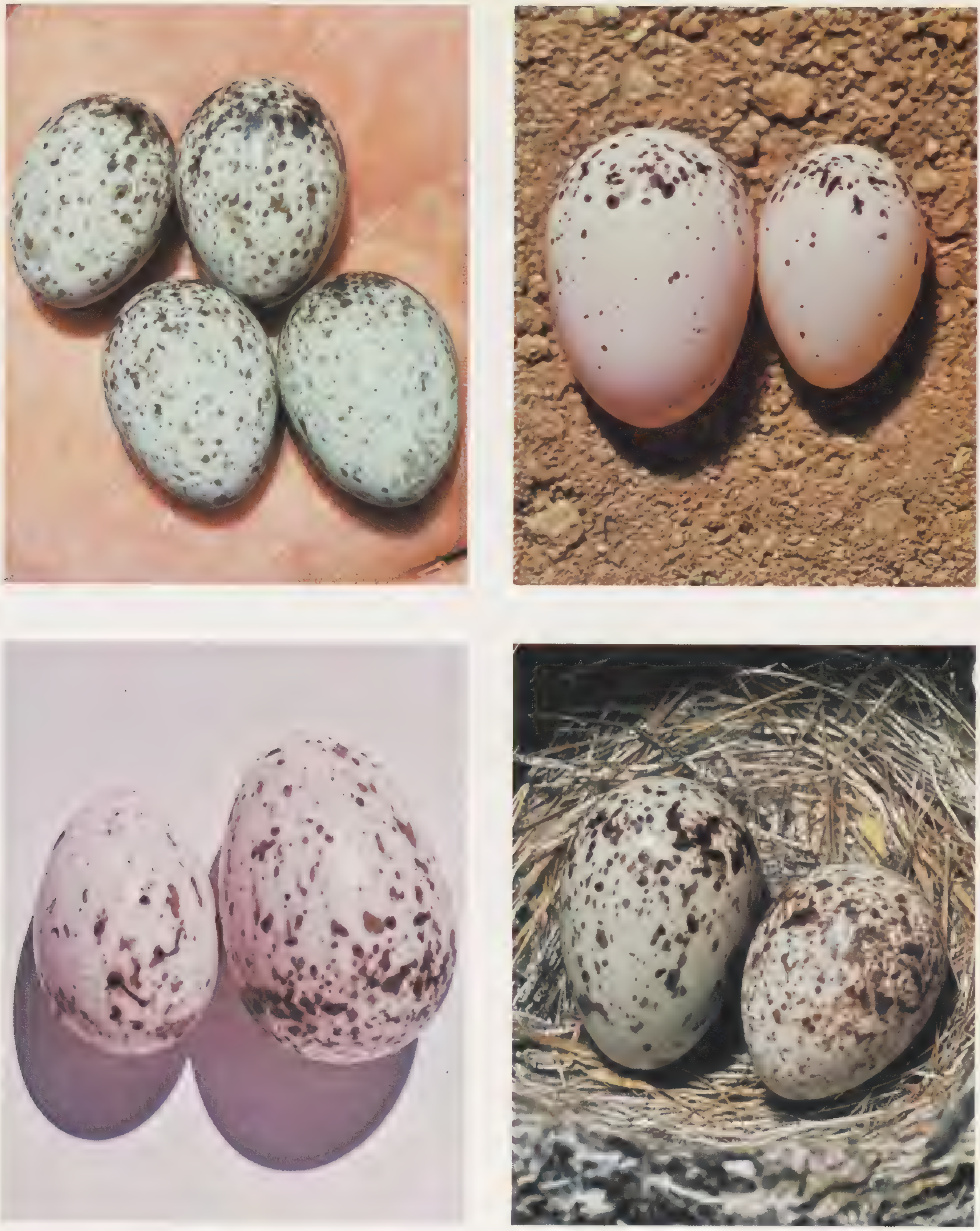

Plate II. These photographs by Rolf Jensen show the similarity of the eggs of the brood parasites and their hosts.

Above left. First Black Cuckoo eggs (two, bottom) authenticated by hatching from a double parasitized nest of Crimson-breasted Shrikes (*Laniarius atrococcineus*). Lower section of Daan Viljoen Game Park, March 1970.

Above right. Parasitized clutch of the Dusky Sunbird (*cinnyris fuscus*), showing excellent color matching of the larger Klaas's Cuckoo egg (left). Klein Spitzkop, April 1971.

Below left. Parasitized clutch of the Dusky Sunbird, showing the excellent mimicry of a Klaas's Cuckoo egg (left). Groot Spitzkop West Camp, April 1972.

Below right. Parasitized nest of the Pririt Flycatcher (*Batis pririt*) by Klaas's Cuckoo at Groot Spitzkop West Camp, February 1971.

Eggs

We characterize Black Cuckoo eggs from our study areas as well-matched to their host's eggs, but usually distinguishable in a given clutch by one or more of the following properties: larger size, more elongate but blunter ends, more finely and uniformly speckled with more grayish than reddish browns, and less tendency to blotching and ring formation of the markings at the thick pole. However, it is clear, even from our material, which is limited geographically and in number of individuals, that the range of variation of host and cuckoo eggs overlaps extensively. This conclusion is strengthened if egg descriptions of this host cuckoo are considered from elsewhere (Hoesch and Niethammer, 1940; Masterson, 1946; quoted with others in Friedmann, 1948). In theory, perfectly matched cuckoo eggs could be found in a nest of this host, as suggested by the parasitized clutch found at Avis Dam in 1974 (Figure 6).

Table 4 gives measurements of shell thickness from a host's and a cuckoo's egg, which suggest that, at least in incubated eggs, it may not be a valid distinguishing criterion (Ottow and Duve, 1965).

Laying, Incubation, and Hatching

In one of the nests found in 1974 (CC74-1B), the cuckoo egg hatched in about 13 days if incubation began on the afternoon of 27 January (after the laying of the last shrike egg), or approximately 13½ days if incubation began immediately after the cuckoo laid in the morning. In another nest (CC74-2), we estimated the incubation period lasted 14 days.

The cuckoo at the Avis Dam nest apparently laid in the morning before 08:30. Few data are available on this point in African cuckoos, but the European Cuckoo (*Cuculus canorus*) usually lays in the afternoon (Chance, 1940), while Masterson's (1946) observations on the Black Cuckoo suggest host-robbing activity, if not laying, in the morning. And Liversidge (1971) indicated egg-laying in the morning for the Jacobin Cuckoo (*Clamator jacobinus*).

Hatching in the 1974 Daan Viljoen nest took place with typical cuckoo rapidity, possibly as little as two hours from first pip.

The Nestling

The development of the Black Cuckoo (Figures 7a to 7f), as described by Skead (1951), was confirmed by our observations, except that the newly-hatched chick is light-colored, turning blackish only after 24 hours or so. Liversidge's (1955) and Reed's (1969) detailed descriptions of the development of the Red-chested Cuckoo apply equally to the Black Cuckoo.

In two nests, host eggs were ejected by young cuckoos between 16 hours and three days old. Data from these and other nests were consistent with previous findings on the duration of the evicting impulse in *Cuculus* (Jensen and Jensen, 1969).

The nestling period of the Black Cuckoo was 20 to 21 days, as in other *Cuculus* (Jensen and Jensen, 1969).

The Black Cuckoo nestling is typical of its genus, and cannot be confused with other species in central South West Africa. Although the nestling of the sympatric African Cuckoo (*Cuculus gularis*) — regarded by some as

TABLE 4

Comparison of Eggshell Thickness in Cuckoos and Their Hosts

				Thickness (mm)[1]			
Nest	*Species*	*Egg measurements (mm)*	*Incubation Stage*	*With membrane*	*Probability level*	*Withous membrane*	*Probability level*
CC71–2	Black Cuckoo (*Cuculus clamosus*)	27.3 × 19.1	¾ term	0.11	>0.05	0.08	>0.05
	Crimson-breasted Shrike (*Laniarius atrococcineus*)	23.8 × 17.4	½ term	0.10		0.09	
PBC71–2	Klaas's Cuckoo (*Chrysococcyx klaas*)	± 18 × 13 (broken)	¾ term	0.09	<0.05[2]	0.08	<0.01[3]
	Pririt Batis (*Batis pririt*)	15.7 × 12.4	¾ term	0.08		0.05	

[1] Average of 10 measurements of thickness in each case.

[2] Significant ($P < 0.05$ of getting difference by chance).

[3] Highly significant ($P < 0.01$).

a race of *C. canorus* — has not been adequately described, and although its hosts and eggs are very poorly known, there is no reason to expect the nestling to differ from that of the European Cuckoo. Hence, naked Black Cuckoos are distinguishable by the pink mouth rather than orange as in the African and Red-chested Cuckoos. Feathered nestlings (Figure 7d) present no problem, being entirely black with leaden-pink legs (Jensen and Jensen, 1969). Cuckoo nestlings are easily told from shrike nestlings (Figure 8) at all stages. Naked nestlings of the Crimson-breasted Shrike are also blackish, but with a much longer bill, prominent yellow gape, orange-yellow mouth, elongate nostrils not raised, and normal passerine foot — cuckoos possess a zygodactylus foot structure, in which the second and third toes extend forward, the first and fourth toes backward.

We recorded weights of cuckoo nestlings as follows: 5 days, 10 gm; 10 days, 37 gm; 12 days, 41 gm (same chick); 14 days, 53 gm; ± 17 days, 55 gm; ± 23 days, 62 gm.

The Fledgling

After leaving the nest, dependence upon the foster parents lasts more than 19 days, and probably for three to four weeks as it does for related species (Jensen and Jensen, 1969). The hand-reared fledgling from Avis Dam was entirely self-sufficient by the 20th day after fledging, but there is no doubt that its education had been forced at a faster than natural rate once it began to fly.

The fledgling resembles the adult except for the initially short tail lacking white tips (Figures 7e, 7f, and 9). The tail lengthens rapidly and is a good aging character. It is about full length by three to four weeks post-fledging. Development exactly parallels that described by Reed (1969) for the Red-chested Cuckoo. Like Reed, we noted some individual variation in the begging call, which becomes louder and more persistent with age, and is typical of all *Cuculus* and *Chrysococcyx* species: a sibilant, un-oiled squeak, occasionally double-noted.

Juveniles probably follow adults independently in their northward migration, but data are difficult to obtain because of the close resemblance between adults and young once the latter have acquired the full tail. The distinguishing whitish tail-tips in adults are inconspicuous in the field. Adults apparently stay much longer (until April) before migrating from South West Africa than from eastern South Africa (Friedmann, 1948; Skead, 1951); but the last birds noted and aged with any certainty have been juveniles in late April. We have banded four nestlings with no returns to date.

KLAAS'S CUCKOO AND ITS HOSTS

Prior to this study, only one published breeding record for Klaas's Cuckoo existed from South West Africa. Kolberg (1966) saw a fledgling fed by a Pririt Batis (*Batis pririt*) in the Waterberg in January 1966. The other hosts that we can now implicate in central South West Africa are: Dusky Sunbird, seven records; Yellow-bellied Bush Warbler (*Eremomela icteropygialis*), three records; and Crombec (*Sylvietta rufescens*), one record. We also have four additional records of the Pririt Flycatcher as host.

Host Breeding Biology

No detailed studies of the above-mentioned host species have yet appeared. We have summarized below the most important relevant features as currently known from our own, and other, records.

Pririt Batis (*Batis pririt*)

This small flycatcher (*Muscicapidae*) measures about 115 mm in length and weighs nine gm. This rather warbler-like bird is common throughout the bushveld areas of South West Africa, to the 100 mm isohyet in the west. However, it ranges and breeds in numbers along the river beds through the Namib Desert right to the coast, where the rainfall averages about 15 mm per annum. It resides in all five study areas and feeds on small insects, some caught in flight, but most gleaned from leaves and twigs.

Breeding occurs in the warmer months, and this flycather does not neccessarily wait for the rains in its inland haunts. (Table 7). It appears to be less dependent on the carry-over effect than the Crimson-breasted Shrike, evidently because of their differing insect diets. Along the Kuiseb River in the Namib, breeding activity is correlated with the river's flood- and temperature-dependent cycle of flowering plants (Jensen, in press).

Territories and territorial boundaries appear rather vague, and this species shows a low degree of nest-site constancy from season to season. The Pririt Batis is distributed rather unevenly in apparently suitable habitats, the exceptions being the high density populations occurring along the rivers of the Namib Desert.

Re-nesting occurs readily, and there is some evidence that two broods can be raised per season, although the vague territoriality, extended post-fledging period, and lack of marked birds made it impossible to be certain.

G. L. Maclean (data from nest record cards) records that both sexes build. Completed nests may remain empty for some time, perhaps awaiting threshold conditions for breeding. Our data and Maclean's indicate that up to five days may pass between nest completion and laying, and longer periods are suspected. Two nests in the eastern Namib remained empty; their respective owners did not nest elsewhere that season as far as known.

Nest and egg data appear in Tables 5 and 6. The nest tends to be well-camouflaged by its exterior decoration of bark chips despite its frequently exposed location on dead branches (Figure 10). Eggs seem to be laid at about the standard 24-hour interval (three records) in the morning — at least once before 06:00 and once between 08:30 and 19:30 for the second egg. Incubation by the female usually begins with the second egg, since only once was a disparity in sibling size noted, and Maclean had a confirming observation. In two nests, hatching of both eggs occurred within 30 and 21.5 hours, respectively. The assumed incubation period of 17 days probably does not differ from that reported for the related Cape Batis and White-flanked Batis (*Batis capensis* and *B. molitor*) by Broekhuysen (1958) and McLachlan and Liversidge (1970). Maclean (nest record card) recorded an incubation period of not less than 16 days.

The nestling period also is not precisely recorded, but is probably 17 days, like the incubation period. A. C. Kemp (nest record card) recorded 17 to 18 days for each of two nestlings. In one of our nests, two chicks left

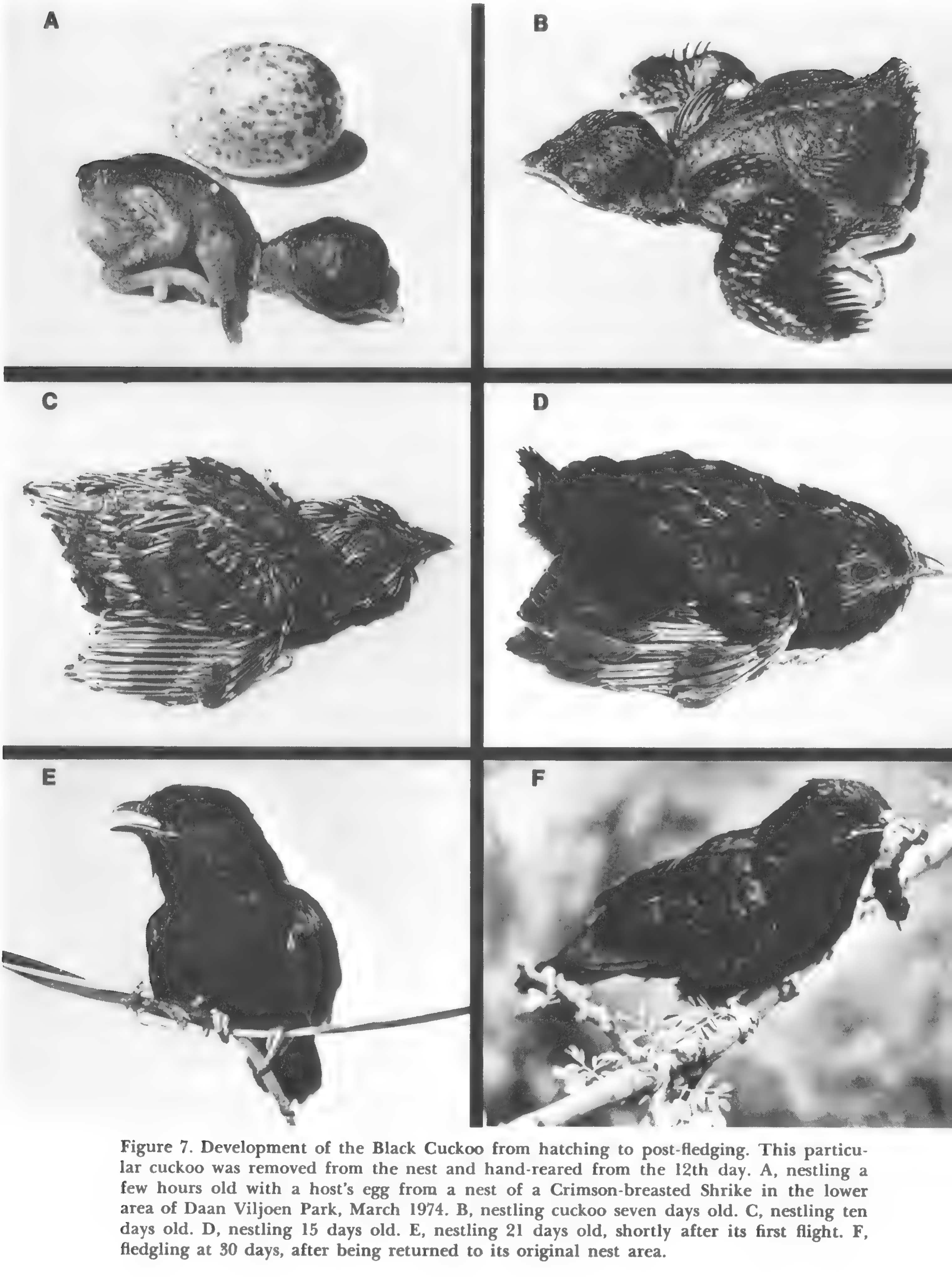

Figure 7. Development of the Black Cuckoo from hatching to post-fledging. This particular cuckoo was removed from the nest and hand-reared from the 12th day. A, nestling a few hours old with a host's egg from a nest of a Crimson-breasted Shrike in the lower area of Daan Viljoen Park, March 1974. B, nestling cuckoo seven days old. C, nestling ten days old. D, nestling 15 days old. E, nestling 21 days old, shortly after its first flight. F, fledgling at 30 days, after being returned to its original nest area.

TABLE 5

Location and Description of Nests of Klaas's Cuckoo Hosts in South West Africa

Species	*Nest site*	*Height (m)*	*Description*	*Dimensions (mm)*
Pririt Batis (*Batis pririt*)	On dead branches or twigs, usually in shade, often openly placed.	1–8; usually 1.5–3	Tiny cup of fine grass, rootlets, and plant fibers neatly bound with spiderweb; plastered on outside with bark chips, occasional pieces of dead leaf, and (2 out of 24 nests) lichen. No decoration on one nest.	60 × 30[1]; inside cup diameter, 40
Dusky Sunbird (*Nectarinia fusca*)	In shrubs, especially spiny *Blepharis gigantea* (Acanthaceae) and *Euphorbia virosa* (26 nests); also non-spiny bushes, shrubs (27 nests).	0.5–2; usually ± 1	Closed oval with side-top entrance under slight hood, attached at back. Greyish dry grass leaves, grass-flower stems, fibers, bound with spiderweb. Lined thickly with silky and downy seed fibers, especially *Stipagrostis* awns, *Pergularia daemia*, other Asclepiads, *Ipomoea* creepers, *Strophanthus amboensis* (Apocynaceae). Outside decorated with light-colored leaves (e.g. *Kissenia*) and *Commiphora* bark shreds.	75 × 125; entrance diameter, 40; inside cup diameter, ± 40–50
Crombec (*Sylvietta rufescens*)	Suspended in open, shaded, and well-shielded spots, as near trunk of spreading tree or bush with drooping branches, creepers, mistletoe, etc.	0.8–7.0; usually 1.2–3.5	Slipper-shaped, suspended by "heel," of leaf stems, flower stems, grass stems, and fibers, with cocoons, animal hair, paper, wasp nests, etc. worked in; bound with spiderweb, lined with fine grass often. Outside decorated with bits of dead leaf, thin bark (as *Commiphora*), dry acacia flowers.	60 × 120 (max.); cup height, (min.) 45–50; inside cup diameter, 32
Yellow-bellied Bush Warbler (*Eremomela icteropygialis*)	Suspended in fork of twigs, usually very open, sometimes well-hidden in foliage.	0.3–1.5	Tiny deep cup, usually whitish, of grass, leaves, cottony and downy plant-seed fibers, bound with spiderweb. Fragile, but thick-bottomed. Downy lining, especially of *Stipagrostis* grass awns, and fine grass stems. Cocoons incorporated often in walls, lining.	50 × 45; inside cup diameter, 30–40

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[1] Horizontal × vertical.

between 15 and 17 days. McLachlan and Liversidge (1970) give 16 to 18 days for Cape and White-flanked Batis.

Nestlings are naked and purplish to blackish brown at hatching. Quills first become visible on the fourth day (Maclean, nest record cards); pin-feathers cover the nestling at eight days; feathers are out of their sheaths five mm on most tracts by 11 days; and the nestling is well-feathered by 14 days. The female broods and both sexes feed the young.

Fledglings resemble the female but are mottled with black on the buffy ocher chest. They are very quiet and unobtrusive, and seem to have an exceptionally long dependence period, during which they gradually differentiate in plumage by losing the black (females) or buffy orange (males) of the chest, and developing the solid chest color of their respectives sexes. Our records show the following regarding length of dependence period: one case more than three, but less than six-and-a-half, weeks; two cases approximately six weeks; one case possibly seven weeks, or possibly a second brood, but less likely because of the late date. We saw that five out of seven single fledglings, whose sex was discernible, followed a parent of the opposite sex.

Dusky Sunbird (*Nectarinia fusca*)

This is one of the smaller sunbirds (Figure 11), about the size of a Pririt Batis (8 gm). It is common in the more arid regions of South West Africa, particularly where flowering shrubs like the Acanthaceae occur in numbers, as along the escarpment. The species also follows the major rivers across the Namib; but unlike the Pririt Batis, the sunbird occurs mainly as a non-breeding, seasonal visitor below, or west of, the 80 mm isohyet. Locally, it may show considerable movement, depending on a food supply that consists largely of nectar and small insects associated with flowers.

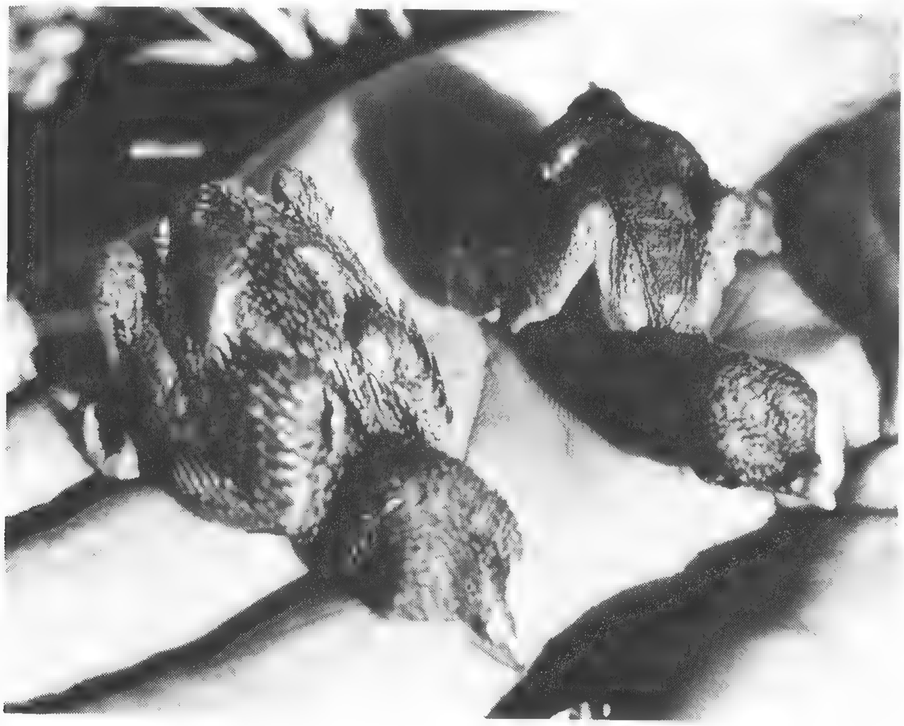

Figure 8. A nestling Black Cuckoo (right) with older Crimson-breasted Shrike nestling from another nest, about four and seven days old, respectively, to show morphological differences of the nostrils, wings, bill, and feet.

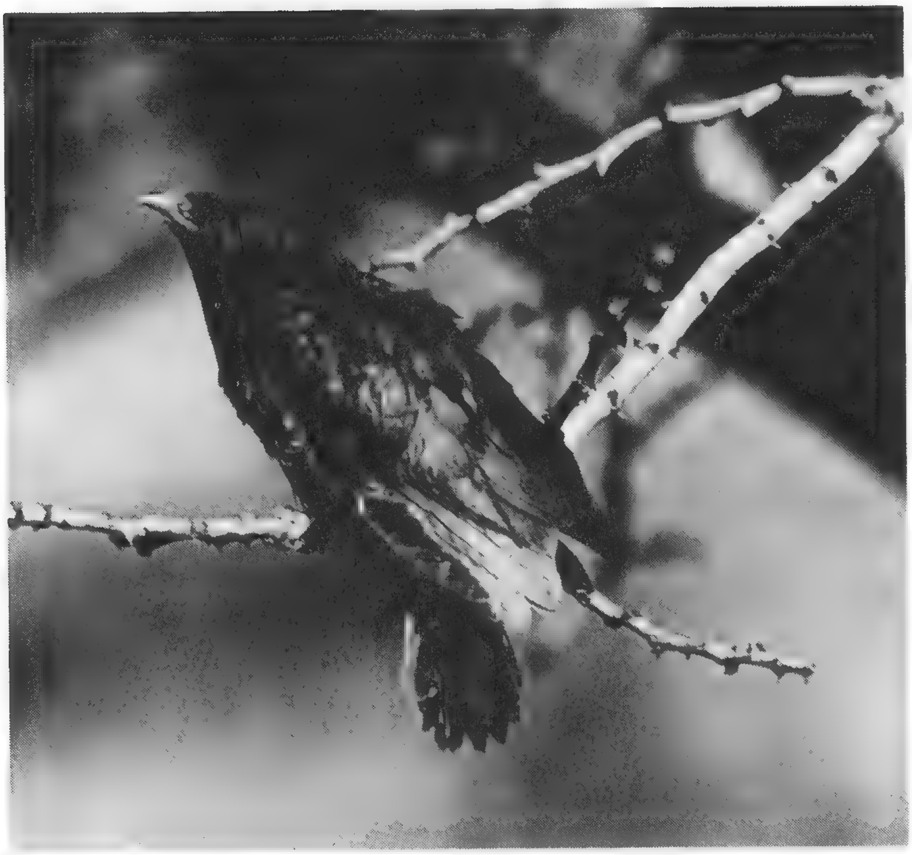

Figure 9. Black Cuckoo just after fledging at Daan Viljoen Park, 26 April 1971.

The Dusky Sunbird seems to breed at any time when food is available; but a distinct peak occurs during the autumn months in our study areas (Table 7). That correlates with the peak flowering period of shrubs in the escarpment and pro-Namib zone (Jensen, unpubl. ms.). We found no nests at Daan Viljoen Park, although the sunbird occurs there and has been recorded breeding in Windhoek 12 km away.

Males sing and move about during the nesting season on well-defined territories that measure about 0.5 to 1.0 hectares in area in the high-density Spitskoppe locality. Both territories and actual nest sites remain fairly constant from year to year. Pairs renest quickly if a nest is lost while conditions are still favorable. At least two broods certainly can be raised in a good year, but our evidence is based entirely on territorial occupancy by unmarked birds.

The female builds the nest, often quite conspicuously placed, but occasionally hidden (Table 5). In one instance, building took six days. We recorded intervals of four to six days between completion and egg-laying (three nest record cards) but suspected this period to be much longer in other less documented cases. Benseler (1970) recorded a period of about 12 days between the start of building and the appearance of the first egg.

McLachlan and Liversidge (1970) and Skead (1967) make the curious statement that "preliminary nests" are built. This misconception apparently arose because (1) nests may be built and then abandoned for various reasons including predation, and (2) laying in completed nests may be delayed, probably in response to environmental factors. We recorded two partially built nests that were abandoned or destroyed by the next visit when we found new nests with eggs five and 25 meters away, respectively. In other cases involving parasitism (detailed later), two nests were built close together within a very short time by each of two pairs of sunbirds.

Eggs are laid on consecutive days according to Benseler (1970), who found the first egg uncovered during the day; but our records of young nestlings often showed an intra-brood variation in size (Figure 12) far more marked than between nest-mates in the Pririt Batis. Broods of two sunbirds sometimes showed a size difference while in three-chick broods, one nestling was usually conspicuously smaller than the other two. It thus seems that incubation may start with the first egg, and usually not later than the second.

Information on eggs and the duration of the nesting cycle appears in Table 6. Clutch size varies, at least in part correlated with environmental variation. The eggs show variability in markings, those from our study areas falling into three broad classes.

Incubation and nestling periods, calculated at 13 days from Benseler's (1970) data and from less complete records of our own, are much shorter than those of the Pririt Batis. McLachlan and Liversidge (1970) give 13 days for incubation and 14 to 15 days for the nestling period in the closely-related White-bellied Sunbird (*Nectarinia talatala*).

The newly-hatched nestling is naked and blackish olive with a relatively long bill and yellow gape. Quills are well developed and the eyes are open at five days. The nestling grows rapidly in contrast to the Pririt Batis, and can leave the nest by 11 or 12 days, if disturbed. Both parents feed, but the female alone incubates and broods.

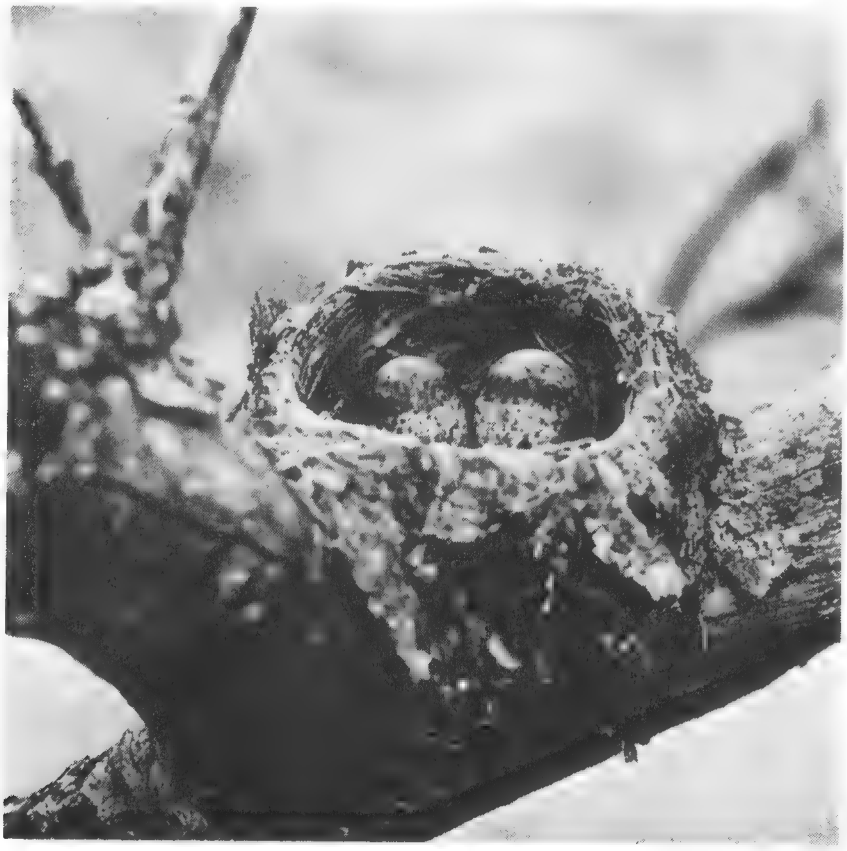

Figure 10. Nest and eggs of the Pririt Batis (*Batis pririt*) at Daan Viljoen Reserve, February 1970.

Fledglings are similar to the mouse-colored female except that the underparts are strongly washed with yellow, and there is a variable amount of black on the throat. Post-fledging dependence, during which both sexes feed the young, lasts at least two weeks and possibly as long as three. Benseler (1970) recorded that the fledglings roosted at night in their old nest for about 12 days. They are quite vociferous in begging from their parents, using a squeaky call not unlike a cuckoo's.

Crombec (*Sylvietta rufescens*)

This warbler, which weighs about 13 gm, occurs commonly throughout the bushveld areas of southern Africa. Only in 1974 was it first recorded as a host of Klaas's Cuckoo in South West Africa, although it is well-known in this capacity in other areas (Jensen and Jensen, 1969). It occurs and breeds along the rivers of the Namib in considerable numbers, and outside of these occurs about as far west as the 100 mm isohyet. Unfortunately no intensive studies of this species or its close relatives seem to have been made.

The Crombec covers a large feeding territory, gleaning insects from foliage and twigs in typical sylviid fashion. It appears to be highly sedentary. Both sexes have a characteristic warbling call that is uttered frequently during the summer breeding season and probably serves an advertising role. Birds along the rivers of the Namib appear to breed earlier than those farther inland (Jensen, in press and in prep.).

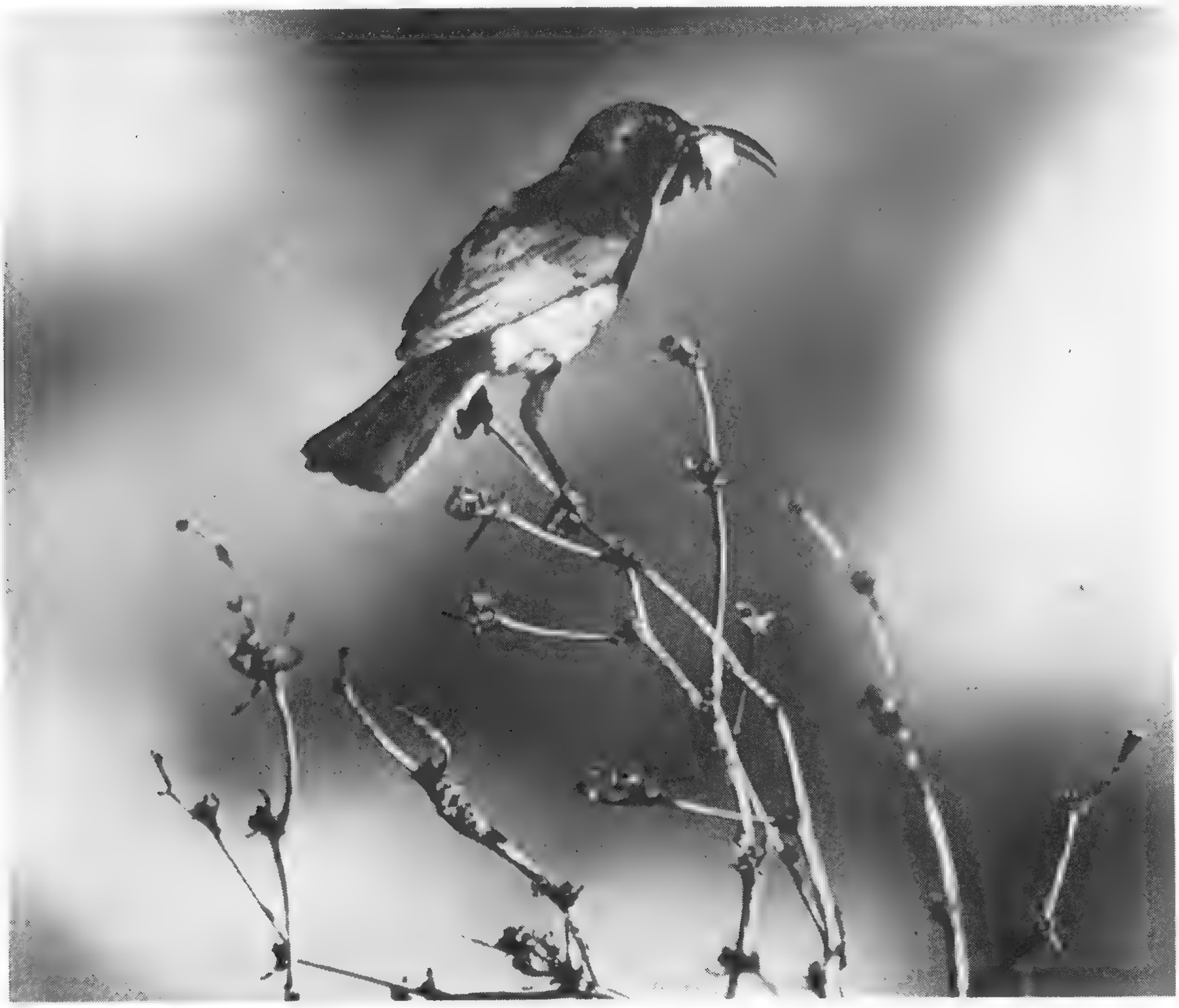

Figure 11. Male Dusky Sunbird (*Nectarinia fusca*) near his nest at Klein Spitskop. This species was one of the common hosts of Klaas's Cuckoo.

Crombecs exhibit a high degree of nest-site constancy from season to season. We have no definite information regarding renesting and second broods, but both are certain to occur under the right conditions.

Information relating to the nesting cycle appears in Tables 5 and 6. Nests, although fairly conspicuous structures, are usually placed in well-hidden sites, such as grottos formed by a spreading tree's down-curving branches. There is no information on the duration of building, but incomplete records suggest that Crombecs are similar to Dusky Sunbirds in this aspect. Seven days elapsed between nest completion and egg-laying in one recorded case.

Eggs apparently are laid on consecutive days (one direct observation). Two nest record cards note disparity in sibling sizes, but others do not, suggesting that incubation sometimes begins with the first egg, but more often with the second. Hatching of a two-egg clutch in one case occurred within 12 hours.

Incubation and fledging periods given by McLachlan and Liversidge (1970) and confirmed by one of our own records are each a day longer than those of the Dusky Sunbird (Table 6).

The nestling develops in the typical sylviid fashion, being initially naked and dark pinkish-olive (turning blackish), with a yellowish gape. On leaving the nest, it is rather quiet and unobtrusive compared with a fledgling sunbird. The post-fledging period is unknown; one of our records indicates it is longer than two weeks. Both sexes feed nestlings and fledglings.

Yellow-bellied Bush Warbler *(Eremomela icteropygialis)*

This tiny warbler (8 gm) is the least known of the four hosts of Klaas's Cuckoo in South West Africa, although it is quite common in the arid zone (80–200 mm rainfall). Farther east, it is less common; but west of the 80 mm isohyet, it ranges all along the larger riverbeds and even the smaller washes in the Namib, and well west of its normal haunts along even the smaller washes. It resides in all five study areas, and its territorial relationships, habits, and food seem to be similar to those of its close relative, the Crombec.

Breeding occurs in summer (Table 7) and its timing probably depends on the rains. Nest site constancy is not apparent. Probably the remarks on renesting and number of broods for the Crombec apply equally to this species. The nest is often astonishingly conspicuous, placed low in the outer twigs of open and even leafless bushes (Table 5).

The meager nesting-cycle data on this species appear in Table 6. Only two-egg clutches have so far been found in South West Africa (McLachlan and Liversidge, 1970). The color resembles that of the sparsely-speckled Crombec egg, except that more olive-brown shades of speckling are common. Eggs are also considerably smaller than the Crombec's.

In one case, eggs were laid on consecutive days, and the bird sat during the day on its first egg. Two chicks in another nest first flew at 15 to 16 days of age. The incubation period, although unknown, is probably the same as the Crombec's.

The nestling is naked at first, with ocher skin, darkening rapidly. Gape and mouth are yellow, the latter becoming more orange with age. There are three black tongue-spots. Like many passerines, including the Crombec, nestlings are prone to leave the nest prematurely if disturbed. The fledgling

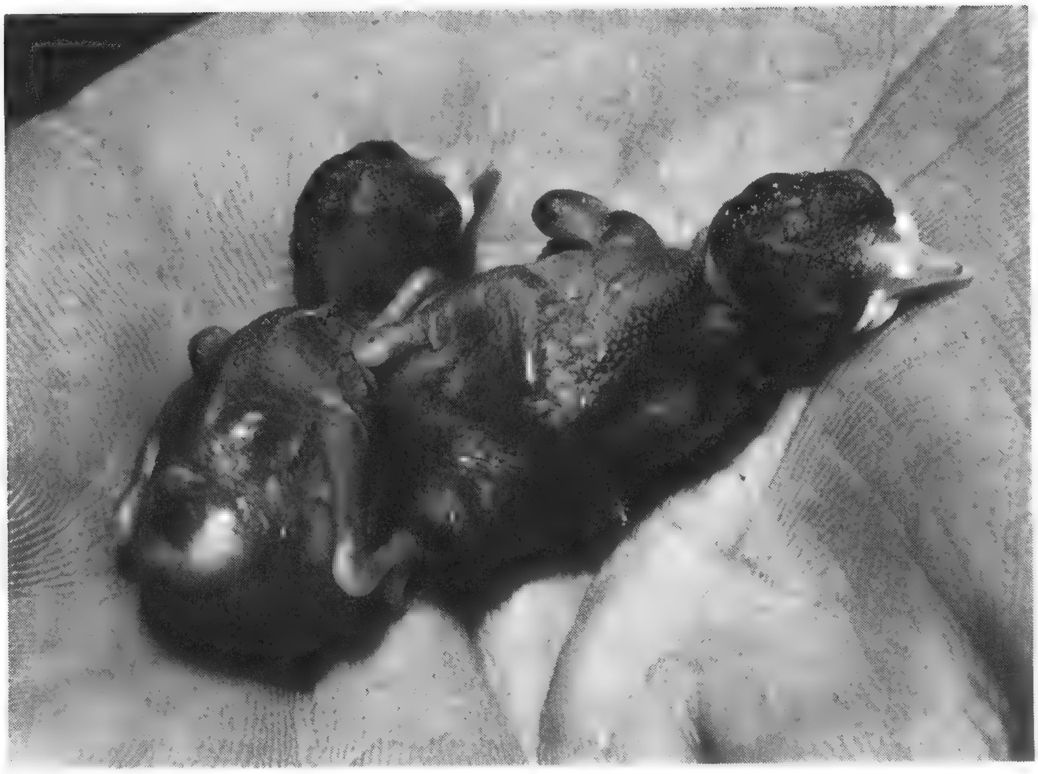

Figure 12. Dusky Sunbird nestlings about two and three days old, showing size disparity within the brood.

resembles the adult except that the belly is only tinged faintly with yellow. There are no accurate post-fledging records, but we saw two independent juveniles with their parents at least four weeks after leaving the nest. Fledglings beg with a quiet but persistent *cheep*, much as in the Crombec.

Breeding Biology of Klaas's Cuckoo

Klaas's Cuckoo is even more of a skulker than the Black Cuckoo, and consequently is unlikely to be noticed when not calling. It appears to be a migrant in South West Africa, arriving in the central parts around November; but its appearance, as determined by calling birds, depends on the rains. Thus at Daan Viljoen Park in the summers of 1968–1969 and 1970–1971, we first recorded this cuckoo in November, but not before January in 1971–1972, and not at all in the summer of 1969–1970, when a widespread drought occurred in South West Africa. At other areas, first records of Klaas's Cuckoo fell in the following months: Djab, November 1968, January 1970, December 1970; Spitskoppe, November 1968, January 1970, February 1971. These records correlated with the onset of adequate rains (Jensen, unpubl. data). In the even more marginal north-eastern Namib Park, it was only recorded in March and April of above-average rainy seasons (1969, 1972, 1973, and 1974).

General features of the breeding biology of Klaas's Cuckoo have been covered by Friedmann (1948, 1968), Jensen and Jensen (1969), MacLeod and Hallack (1956), and Skead (1952). Briefly, this cuckoo follows the *Cuculus* pattern. Males call from more or less defined territories, but Skead's (1952) feeling that they shift territorial boundaries during the season is strongly supported by our observations. Pairing relationships are

TABLE 6

Clutch Size, Eggs, Incubation, Fledging, and Post-fledging Periods in Klaas's Cuckoo Hosts

Species	*Clutch size*[1]	*Egg description*	*Egg measurements (mm)*	*Incubation period (days)*	*Fledging period (days)*	*Post-fledging dependency (days)*
Pririt Batis (*Batis pririt*)	2 (21 records)	White, greenish or buffy, usually heavy speckling and blotching in brown shades (mostly reddish) concentrated at thick end. Sometimes underlying bluish slate or bluish brown markings; or sparse markings.	15.7–18.1 × 12.0–13.2; average 16.5 × 12.6 (19 eggs from study areas)	17	17	±42
Dusky Sunbird (*Nectarinia fusca*)	2 (6 nests) 3 (14 nests)	All eggs white background. *Type 1:* Sparse blackish brown to slaty black speckling, fine or coarse, discrete or streaked, mostly at thick end. No blotches (17 clutches). *Type 2:* Small light brown, often dense speckling, sometimes streaked, concentrated at thick end (5 clutches). *Type 3:* Medium to red-brown or even slaty brown, often pale, markings, all sizes; often streaked, covering most of egg, slightly more at thick end (3 clutches).	15.0–16.1 × 10.6–11.6; average 15.5 × 11.1 (10 eggs from study areas)	13	13–14	±20
Crombec (*Sylvietta rufescens*)	2 (8 nests) 3 (3 nests)	White, sparsely speckled in shades of brown, from olive to dark slaty brown, but usually reddish, concentrated at thick end. Occasionally heavily speckled and blotched all over (2 of 8 clutches.) One clutch with underlying gray speckles (Hoesch and Niethammer).	17.8–18.9 × 12.3–13.5; average 18.4 × 12.9 (11 eggs from S.W.A.)	14	14	>14
Yellow-bellied Bush Warbler (*Eremomela icteropygialis*)	2 (6 nests)	White, very sparsely speckled, mostly at thick end, sometimes in ring, with brown in shades from greenish or olive to red and dark brown. Sometimes more speckling.	14.7–15.3 × 11.2–11.5 (4 eggs from S.W.A.); 14.2–16.8 × 10.0–12.2 (34 eggs all races)[2]	14	15	>14

[1] From nests visited more than once up to hatch day, if not maximum clutch first visit.
[2] McLachlan and Liversidge (1970).

obscure in this species; but females apparently come to calling males, and courtship feeding often has been noted. Egg-laying has not been observed It would seem that a female Klaas's Cuckoo could not get into a Dusky Sunbird's nest to lay.

The eggs have been considered in various instances to have no, little, and "a fair degree" of resemblance to host eggs (Friedmann, 1968) but many were probably misidentified. Jensen and Jensen (1969) reported a Crombec's nest in Rhodesia, in which an experienced observer (C. J. Vernon) could not distinguish between cuckoo's eggs and host's eggs.

One egg is usually laid per nest. Jensen and Jensen (1969) speculated that incubation and fledging periods were 11 to 12 and 15 to 21 days, respectively. Eviction occurs in standard fashion (MacLeod and Hallack, 1956) and nestlings show typical *Cuculus* features. Identification of eggs and young frequently has been problematic in areas where other *Chrysococcyx* occur. Jensen and Jensen (1969) found no data on the post-fledging period. Fledgling Klaas's Cuckoos behave in typical cuckoo fashion, begging persistently with a husky sibilant *tseep*. New data are presented below on various aspects of the breeding biology of Klass's Cuckoo. Most of the observations came from Spitskoppe, which formed a "twin island" habitat for Klaas's Cuckoo and one of its major hosts, hence a particularly favorable observation locale.

Territory

At Klein Spitskop there appeared to be only one pair on the east side study plot, where a single male called. All cuckoo eggs found were very similar and probably laid by one bird. The male called over an area of at least 30 hectares along the base and up the slope of the mountain. We found eggs of the female over an area of about 16 hectares within the male's calling territory, but the possibility that she may have laid outside the study plot (about 20 ha) cannot be ruled out.

At Groot Spitskop and Bushman's Paradise, a number of males called. There appeared to be only one calling male in the West Camp study plot, where eggs of two females were found. Although none of the territories of these males fell completely within a study plot, it seemed that these males, and others, called over areas at least as large as at Klein Spitskop. In 1974 we followed a calling male in northeastern Namib Park over an area of about 12 hectares during a morning. Allowing for territorial shifts, he could easily have dominated two or three times that area in a season. A calling male at Avis Dam (1974) moved in a period of four weeks over about 50 hectares, but there is no certainty that it was the same bird, although we heard only one cuckoo calling at a time.

If we assume that 16 hectares was the female's laying territory at Klein Spitskop — that is, the area in which she deposited eggs in the nests of hosts — she could parasitize about 10 to 12 sunbird pairs (of a potential 15 to 20 maximum, reduced by nest-site availability and other factors).

Courtship and Pairing

We have little data on courtship and pairing. We saw the Klein Spitskop cuckoos together several times; we never spotted the female alone. On one occasion, we noted the male courtship-feeding the female with a bright red (distasteful) *Probergrothius* sp. nymph, a bug specifically associated with *Sterculia* trees in the area. One such tree was a regular call-post. Courtship feeding with the usual caterpillars (scarce at Spitskoppe) was observed at Ameib and Djab.

Breeding Season

The calculated or estimated egg dates of Klaas's Cuckoo and its hosts in the study areas between 1968 and 1972 are shown by half-months in Table 7. The cuckoos seemed to confine egg-laying to January through April, inclusive, although Kolberg's (1966) Waterberg egg-date fell in December. The hosts laid their eggs between the second half of September and the first half of June. If we consider only areas where Klaas's Cuckoo occurs and exclude the records of the Namib rivers, 27 out of 120 egg dates of the hosts (23%) fell outside the cuckoo's maximal season span in the four-year period.

Since the hosts' breeding seasons differ (Table 7), it is to be expected that different cuckoo *gentes* will show adaptation in this direction, but the data are too few to discuss at present. A gens is a host-specific tribe of cuckoos laying an egg-type which mimics its host's. The breeding season of Klaas's Cuckoo, as given for South West Africa by Jensen and Jensen (1969), must now, at any rate, be extended to the third quarter of April, with the last fledgling seen on 30 May.

Clutch Size and Laying

In 1971 we found three Klaas's Cuckoo eggs in Dusky Sunbird nests at Klein Spitskop. We also found a fledgling cuckoo with a fourth pair of Dusky Sunbirds in the cuckoo's territory. We calculated egg dates to have been 18 March and 10, 17, and 23 April. At Groot Spitskop in 1972, one female was probably responsible for two records with estimated egg dates of 12 and 14 April in sunbird nests about 600 meters apart. Payne (1973) concluded from histological and macroscopic examination of ovaries that, in Klaas's Cuckoo, females laid eggs on alternate days in clutches of two to four with longer periods between clutches.

We observed no instances of laying by the cuckoos, but the following two cases at Klein Spitskop suggest characteristics of the egg-laying behavior:

(1) A pair of Dusky Sunbirds (Pair NB) built a nest in which one cuckoo egg was being incubated on 15 April 1971. The egg appeared to be in an advanced state of development. This nest was empty, but intact, on 19 April. On 28 April a new nest five meters away contained a sunbird egg, but on 15 May it, too, was empty although undamaged. Successful broods were raised in this territory in 1969 and 1972.

(2) Pair NFK raised at least one brood in 1972 and probably one in 1969. In 1971 an egg, fresh laid, was found on 15 April. On 19 April the nest was empty but intact and a completely new nest, possibly overlooked on the 15th, was found empty 10 meters away. On 28 April the original nest held a cuckoo and a sunbird egg. The cuckoo fledged successfully. The second nest was never used as far as could be determined.

It appears that the cuckoo usually removes a host's egg when laying. Disappearance of eggs with neither visible nest damage nor substitution of

TABLE 7

Egg Dates[1] of Klaas's Cuckoo and Hosts in Study Areas 1968–1972

Host species and year	September		October		November		December	
	1–15	16–30	1–15	16–31	1–15	16–30	1–15	16–31
Pririt Batis (*Batis pririt*)								
1968–1969		1(NK)[2]	3(NK)	1(NK)	2(NK)	1(S)		
1969–1970				2(NK) 1(A)	1(NK)	1(NK) 1(V) 1(A)	1(NK)	
1970–1971		2(NK) 1(A)	1(NK)			1(A)	1(D)	1(V)
1971–1972	(No egg dates available — only V and S checked)							
Dusky Sunbird (*Nectarinia fusca*)								
1968–1969						1(D)		
1969–1970								1(S)
1970–1971								
1971–1972								
Crombec (*Sylvietta rufescens*)								
1968–1969		2(NK)			1(NK)	2(NN)		
1969–1970							1(V)	
1970–1971								
1971–1972								
Yellow-bellied Bush Warbler (*Eremomela icteropygialis*)								
1970–1971		1(NK)			1(V)			1(D)
1969–1970	(No egg dates available)							
1968–1969						1(V)		
1971–1972								

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[1] Calculated or estimated to half-month in which cuckoo egg and last egg of host clutch, respectively, were laid.

[2] Letters in parentheses indicate the following locations.

NK = Namib Park, Kuiseb River at Gobabeb and Swakop River (lower).

NN = Namib Park, northeast and eastern hills.

[3] Figure following slash indicates number of cuckoo eggs.

S = Spitskoppe

A = Ameib

D = Djab

V = Daan Viljoen Game Park

January		February		March		April		May		June	
1–15	16–31	1–14	15–28	1–15	16–31	1–15	16–30	1–15	16–31	1–15	16
1/1(V)[3]	1(D)										
1(NN)	1(V)	1/2(D) 1(V)	3(V)	1(V)							
1(V)		5(A)	1/1(S) 1(A)	1/1(S) 1(NK) 2(A)	1(A)						
		1(A)	4(S) 1(D)	2(NN) 1/5(S) 1(D) 1(A)	3(S)	4(S) 2(NN)	1(A)	2(S)	3(S)	1(S)	
	1(A)	2(A)	2(A) 1(S)								
				2(S)	1/1(S)	1/3(S) 2/5(S)	2/6(S) 1(NN) 3(S)	1(S) 1(S) 1(A)	1(S)		
1(NK)	1(D)							1(S)			
	1(A) 3(V)	1(A)	1(D)	1(A)							
		1(NN) 1(S) 1(D)	1(A)	1(S)			1(NK)				
						1(S) 1(A)					
					1(S)						
				1(NN) 1/1(S)							
	1/1(V)										

cuckoo eggs may possibly be accounted for by female cuckoos which, though not ready to lay, instinctively go through the associated motions of parasitizing a nest. Such behavior could have a selective advantage since it would tend to cause renesting by the host, and hence a second chance for the cuckoo (Chance, 1940). However, if this form of predation occurred in the above cases, it is difficult to explain the removal of the cuckoo's egg from Pair NB's nest unless the sunbird threw out the egg. An experiment (Jensen, unpubl. data) revealed that another sunbird, the Scarlet-chested (*Nectarinia senegalensis*), discriminates on the basis of egg color. In the above case this seems rather unlikely since the egg was well developed and would have matched the specific female's eggs quite well in color. Nonflying predators seem to be ruled out since both nests were virtually impregnably situated in spiny *Blepharis gigantea* shrubs.

Eggs

We found no Klaas's Cuckoo eggs at Daan Viljoen Game Park, Djab, or the Namib Park, but obtained four nestling and fledgling records. At Spitskoppe, we found eggs in Dusky Sunbird and Pririt Batis nests (Table 8). Three females appear to have been involved. Three eggs were found on the Klein Spitskop study plot in 1971, and were so similar that they must have come from one female (Plate II). The two eggs from Pririt nests at the West Camp study plot, Groot Spitskop, were found about 500 meters apart and were also similar enough to have come from one female (Plate II). Finally, the 1972 egg from a Dusky Sunbird nest at West Camp was different from both the other Klaas's sets, and in many respects intermediate (Plate II). It was found in a nest only 60 meters from the 1971 site of parasitized Pririt nest PBC 71-1. The cuckoo eggs were authenticated as shown in Table 8. One of the Klein Spitskop eggs disappeared, but can safely be accepted because of its close similarity to the other two eggs from that study plot. The identity of the 1972 egg is beyond doubt because of the young embryo's cuculine morphology, and by size and shape criteria (Jensen and Jensen, 1969). The only possible source of confusion, the Didric Cuckoo (*Chrysococcyx caprius*), furthermore has never been seen at Spitskoppe, and its hosts are different (Kemp, *et al.*, 1972).

The six egg, described in Table 8, differ somewhat from previously described Klaas's eggs from southern Africa (Jensen and Jensen, 1969). They also extend the known range of measurements of authentic eggs given in that paper to a maximum width of 13.8 mm, but fall within the suggested product factor (length × maximum breadth) limit of 270.

From Table 8 and the illustrations, it can be seen that color matching of parasite and host eggs was invariably good to excellent, despite the inter- and intra-species differences in host eggs.

Thickness of eggshells from an incubated Klaas's Cuckoo egg and a Pririt Batis egg (one of each) is given in Table 4. In contrast to the Black Cuckoo, there appears to be a significant difference between host and parasite.

Incubation and Hatching

Below, we have summarized incubation period and hatching data from a parasitized nest (CK 71-2) of a Dusky Sunbird at Klein Spitskop:

15 April 1971, 09:30 — One sunbird egg;
19 April, 16:00 — One sunbird and one cuckoo egg (see Table 8 and Plate IIb);
28 April, 07:00 — Still two eggs, no sign of pipping; 11:00 — Cuckoo nestling completely dry, no sign of egg-shell.

The data suggest a maximum incubation period of 12 days for this Klaas's Cuckoo egg, taking into account the observed incubation behavior and other relevant factors. It is noteworthy that the cuckoo hatched before the sunbird, whose incubation period is 13 days.

Once again, this case demonstrates the remarkably rapid hatching period of cuckoos. An incubator-hatched Didric Cuckoo showed the same phenomenon.

The Nestling

No adequate descriptions of the Klaas's nestling seem to be available. The information at our disposal from several nest record cards and a hand-reared nestling (from nest CK-69) indicates that it conforms in detail to the development of the Black Cuckoo. The newly hatched nestling (Figure 13a) is a yellowish olive-brown, not pink like the Didric, but with pinkish translucence in places, and slightly darker dorsally. The one from nest CK 71-2 weighed 1.8 gm. At 48 hours, the nestling is mostly dark olive to blackish, more like a Didric of the same age, but with a blackish and horn-colored bill. Didric's is orange to red. All features typical of *Cuculus* nestlings are present. The mouth interior is bright orange. Further development is illustrated in Figures 13b to 13e. Eyes open at about six days. Preening was first seen at about day nine and becomes a major activity by day 14. The iris is gray-brown; legs are blackish.

The cuckoo was taken from the nest (CK-69) at about nine days of age and hand-reared. It appeared to develop normally on a nearly natural diet and flew at 20 to 21 days. At one nest a cuckoo took more than 16 days to fledge, and all records were consistent with a 20-day fledging period. We confirmed the occurrence of typical cuculine eviction.

Intruder reaction is exactly as in *Cuculus* and the Didric Cuckoo. After about a week, nestlings begin to gape and lunge at an intruder, erecting their quills or feathers. If handled, they produce the typical nauseating, oily black and brown defense fluid from the cloaca, usually defecating simultaneously. Observations suggest that this fluid is as repulsive to the bird as to its molester.

The Fledgling

Like the Didric, Klaas's Cuckoo has a protracted period of dependence on the foster parents after fledging. The hand-reared cuckoo (Figure 13e) left when 10 days "out of the nest," but probably was not self-sufficient then. One nest (PBC 71-1) yielded a fledgling cuckoo last seen with foster parents when about 25 days out of the nest, at which time it was still begging and being fed.

On leaving the nest, young Klaas's Cuckoos can easily be caught on the first day or two. They are conspicuously short-tailed, very tame, and possess very limited flying ability. One such bird weighed 17.5 gm. By about 7 to 10 days out of the nest, the tail is more or less full length and the bird can

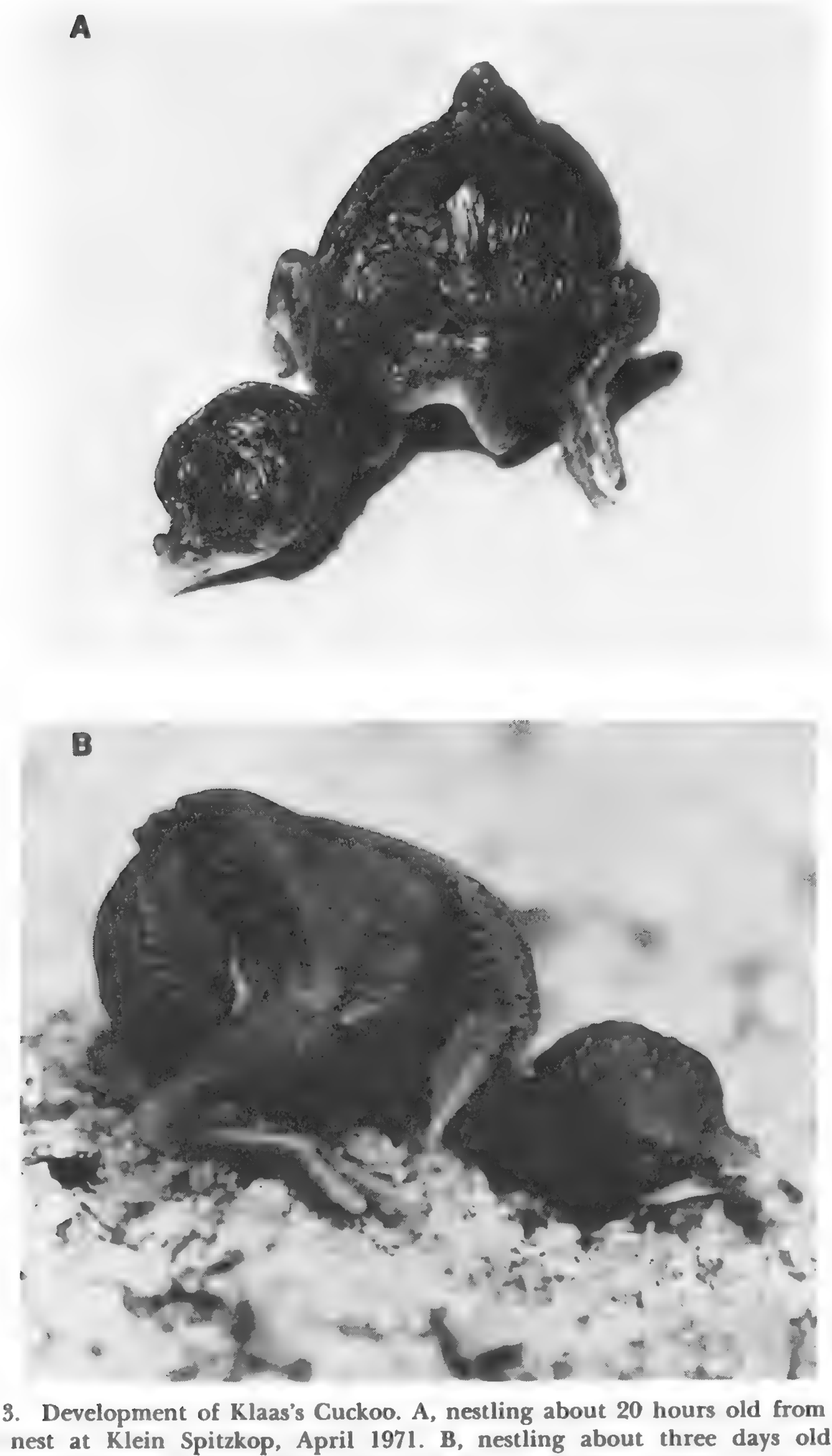
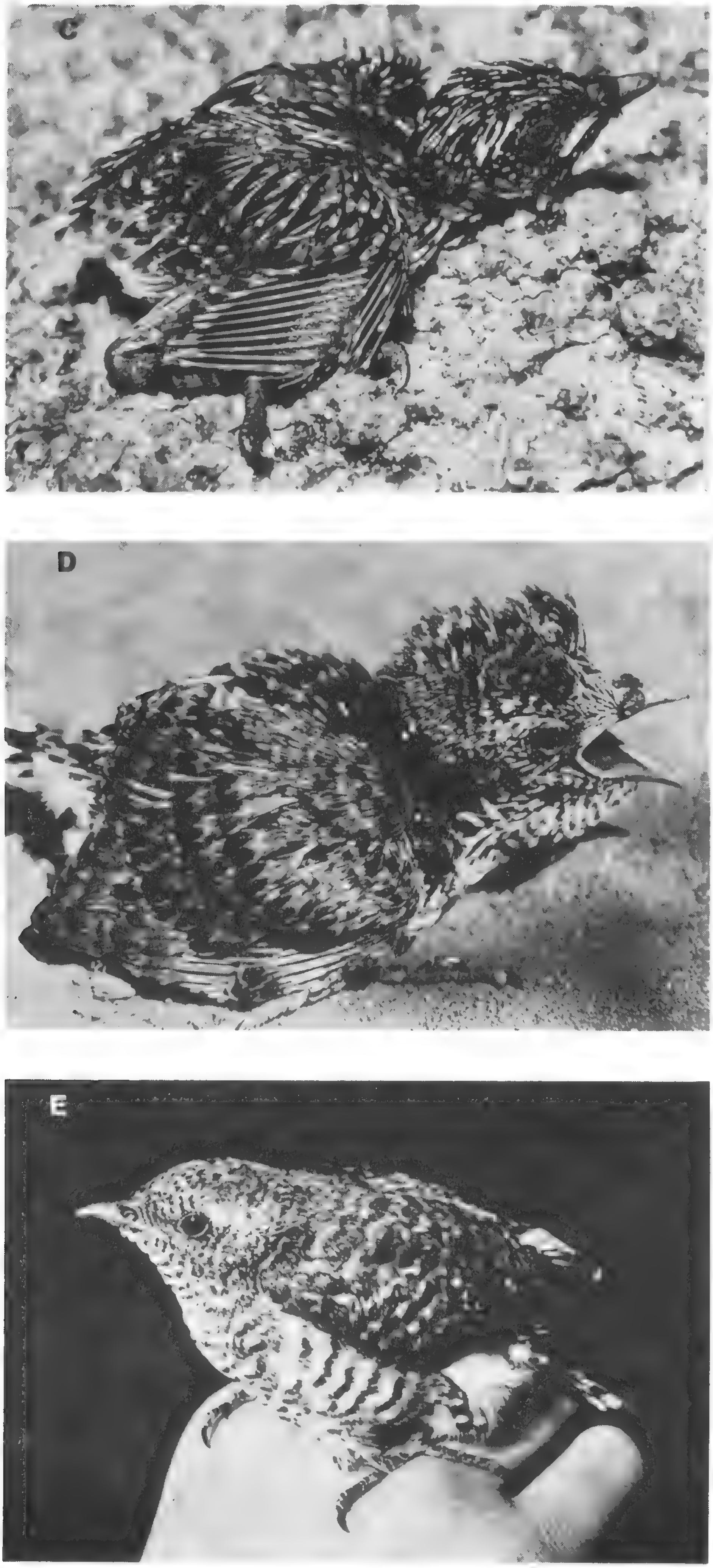


Figure 13. Development of Klaas's Cuckoo. A, nestling about 20 hours old from a Dusky Sunbird nest at Klein Spitzkop, April 1971. B, nestling about three days old from a Dusky Sunbird nest at Klein Spitzkop, March 1969. C, nestling at about 10 days. D, hand-reared nestling at about 13 days old. E, hand-reared cuckoo at about 24 days, four days after its first flight.


C
D
E

fly quite well. Almost at once, it starts molting into adult plumage, primarily by losing to some extent the barring below. Males also turn greener.

We banded four young, and subsequently saw two of them during their post-fledging dependence period.

Discussion

Cuckoos are an especially difficult group to study ecologically, although a few observers have done so with remarkable success (Chance, 1940; Liversidge, 1971). The data presented in this paper explain why, at least in the Black Cuckoo, so little information has been available so far. This species is a highly specialized, one-host brood parasite in central South West Africa, showing all the adaptations to this niche that have been demonstrated for host-specific populations of the European Cuckoo. Although the actual sequence of egg-laying has not been observed, available data now suggest that it must be virtually identical to the procedure in the European Cuckoo: close observation of host nests; careful synchronization of laying time with that of the host; restriction to one egg per nest, usually substituted for one host's egg; and the inevitable "slip-ups" when two females occasionally lay in the same nest. The eggs match those of the host very closely, given the minor host-egg variations. They must have been overlooked numerous times in the past by bird-watchers, ornithologists, and zoologists; a possible example is "shrike" clutch 91, page 299 of Hoesch and Niethammer (1940).

In the case of Klaas's Cuckoo, a slightly different picture emerges. It, too, conforms to the classic *Cuculus* pattern more than previously realized, but, unlike the Black Cuckoo, it has adapted to multiple hosts. Its eggs in central South West Africa have evolved a close mimetic resemblance to those of at least two regular hosts, although the egg records are all from one small area so far. In fact, two classic *gentes*, parasitizing and egg-mimicking two different hosts, occur side by side at Spitskoppe, a situation not previously known for any African cuckoo except the Didric (Jensen and Vernon, 1970; Payne, 1967). Another difference between Klaas's and Black Cuckoos is that the eggs of Black Cuckoos frequently match rather closely those of their host in size. The eggs of Klaas's Cuckoos, on the other hand, are frequently twice the volume of their hosts' eggs (Plate II).

Rates of Parasitism and Breeding Season

A particularly intriguing aspect of the ecology of brood parasites concerns the rate of parasitism. It is useful to distinguish between the overall parasitism frequency, and local, temporally circumscribed parasitism rates or "incident frequency" as defined by Jensen and Vernon (1970). A comparison of these various figures for the two cuckoos under discussion appears in Table 9. We conclude that (1) the two species have different approaches to balancing the equation; (2) overall parasitism rates need not be extremely low (Lack, 1963, on the European Cuckoo); (3) different hosts suffer to different degrees, both when different cuckoos and different hosts of one cuckoo species are compared; and (4) the incident level of parasitism differs greatly at different times and places. It should be noted, however, that parasitism rates of the Black Cuckoo for all of South West Africa in Table 9 may be biased upwards, since many records of eggs only for the host were ignored as indeterminate.

TABLE 8

Egg Records of Klaas's Cuckoo with Hosts in Central South West Africa

Host species and nest number	*Host egg measurements (mm)*	*Description of host egg*	*Parasite egg measurements (mm)*	*Description of parasite egg*	*Cuckoo's fate*
Pririt Batis (*Batis pririt*) PBC71–1	16.0 × 12.4	Buffy-white, heavily and finely speckled red-brown, concentrated in ring at thick end.	19.2 × 13.1	Pale whitish green, with dark brown, red-brown, and light brown speckling sparse at thin end, concentrated in ring at thick end.	Hatched, flew.
PBC71–2	15.9 × 12.4 15.7 × 12.4	White, heavily speckled and blotched dark and medium red-brown, few cloudy mauve-brown underlying marks; all concentrated at thick end.	(broken)	Pale greenish white, speckled and blotched dark red-brown and dark brown concentrated in ring at thick end.	Three-quarters-developed embryo, abnormal, dead.
Dusky Sunbird (*Nectarinia fusca*) NB71–1	—	White, sparsely marked with scrawls, speckles, streaks, blackish, mostly thick end. Type 1.[1]	18.4 × 13.7	White, sparsely speckled with dark slaty brown round speckles and spots, mostly at thick end.	Egg disappeared.
CK71–2	15.7 × 10.9	White, sparsely marked, almost all at thickened, with blackish slate streaks, blotches, spots, in a ring. Type 1.	18.9 × 13.4	Whiter white than host's, markings very similar but very dark brown and slaty brown rather than black.	Nestling, removed, preserved, chromosomes.
NF71–1P	15.7 × 11.1	White with cast from yolk and embryo, sparsely marked more or less in ring at thick end with scrawls, streaks, speckles and streaky blotches of brownish black. Type 1.	18.9 × 13.8	Whiter white than host's, sparsely speckled with discrete dark brown and few underlying slate brown marks almost all at thick end.	Hatched, ringed, flew.
NF72P	15.5 × 10.8	White, sparse pale reddish brown and slaty brown speckles and streaks and few blotches, somewhat concentrated at thick end. Type 3.	19.4 × 13.4	White, speckled with various-sized marks of medium red-brown and darker and lighter brown, concentrated in ring at thick end.	Removed for egg-white and embryo analysis (see text).

[1] A re-nesting in the same territory; information from Nest Record Card NB71–2.

Several factors play a role in maintaining the balance at a relatively low level of parasitism, including geographic range, host behavior, and timing of breeding seasons.

The two cuckoos range over a geographic area smaller than their hosts' distributions. Thus, Crimson-breasted Shrikes occur farther west and south than Black Cuckoos. The four hosts of Klaas's Cuckoo likewise extend much farther into the Namib Desert as breeding species than does their parasite (see Tables 7 and 9); they also occur southwards beyond its range.

Different pairs of a host species vary in sensitivity to disturbance and probably in discriminative ability (Victoria, 1972, on ploceids). Thus, one pair of Crimson-breasted Shrikes at Daan Viljoen Park apparently raised a brood in only two years out of five, due to desertion or self-destruction of nests as a result of interference by cuckoos, and possibly humans in one case. In one year, two successive nests of the same pair were parasitized and failed. Another pair in an adjacent territory, where Black Cuckoos frequently called, escaped parasitism in four years as far as we knew. A third pair about 1.5 km away was parasitized three out of four years. One or more Black Cuckoos successfully parasitized this pair twice, and once two females laid two eggs in the same nest. The pair of shrikes that laid white eggs was never parasitized successfully in four years. Similar observations concerning sunbirds were made at Spitskop, where, for example, one vulnerable pair was parasitized twice in one year, while adjacent pairs escaped altogether.

Host breeding seasons are longer than the cuckoos' (Tables 1 and 7), thereby ensuring that many broods have a 100 percent chance of avoiding parasitism. Possibly even more important, the longer breeding season provides regularly parasitized pairs with a chance of raising one or two unparasitized broods per season under these circumstances, as exemplified by the 1974 Avis Dam shrikes (Table 3). This would help to conserve the parasitism-prone genotype(s).

Cuckoos are rather specialized caterpillar feeders, and it seems certain that the primary limiting factor involved in their seasonality of occurrence and breeding is food. In central South West Africa, rising temperatures in spring produce "blooms" or "flushes" of adult insects of many winged forms that apparently undergo the winter in a post-larval resting stage. These insect blooms are accompanied by the flowering of several dominant trees, especially *Acacia* spp, and the leafing of some trees (Jensen, in prep.). However, only with the first significant rainfalls (usually November and December) do leafing and growth become general for trees, various shrubs, herbs, and grasses. It is at this stage of the vegetation cycle that insect larvae, especially caterpillars, become abundant, thus providing adequate food for cuckoos. Adult insects continue to occur at higher average levels in flushes closely correlated with the rainy spells and accompanying temperature fluctuations. By April — but extremely variable from year to year — the larval forms have greatly declined in numbers and rains have usually ceased; but adult insect blooms still occur during warm spells. Thus it is possible for insectivores eating primarily adult insects to breed both earlier and later than their cuckoo parasites, especially in good years when rainfall is above average. Under these conditions, the advantages of multiple broods, especially to a consistently parasitized pair, are obvious, and there is evidence of multiple broods in most host species mentioned.

TABLE 9

Parasitism Rates of Black and Klaas's Cuckoos in South West Africa

	Daan Viljoen Park	Ameib	Djab	Spitskoppe	Namib Park (northeast)	Total cuckoo areas, 4 years	Total study areas, 4 years	All South West Africa, all-time[1]
Cuculus clamosus with:								
Laniarius atrococcineus								
1968-1969	—[2]	—	X[3]	X	X	—	—	[0/1][4]
1969-1970	3/7[5]	0/?	X	X	X	3/7	3/7	[3/8]
1970-1971	5/10	0/3	X	X	X	5/13	5/13	[5/14]
1971-1972	1/6	—	X	X	X	1/6	1/6	[1/6]
All-time	10/25	0/3	X	X	X	10/28	10/28	14/39
	40%	0%				36%	36%	36%
Chrysococcyx klaas with:								
Batis pririt								
1968-1969	1/1	0	0/1	0/1	0	1/3	1/10	
1969-1970	0/7	0/2	1/3	0	0/1	1/13	1/17	
1970-1971	0/2	0/11	0/1	2/2	0	2/16	2/21	5/76
1971-1972	—	—	—	—	—	—	—	7%
Total	1/10	0/13	1/5	2/3	0/1	4/32	4/48	
							8%	
Nectarinia fusca								
1968-1969	X	0/3	0/3	1/22	0/4	1/32		
1969-1970	X	0/5	0	0/2	0	0/7		
1970-1971	X	0	0	4/14	0	4/14		7/84
1971-1972	X	0/1	0	2/9	0/1	2/11		8%
Total	X	0/9	0/3	7/47	0/5	7/64	7/64	
							11%	
Sylvietta rufescens								
1968-1969	—	0	0/1	0/1	0/2	0/4	0/8	
1969-1970	0/4	0/3	0/1	0	0	0/8	0/8	
1970-1971	0	0/1	0/1	0/2	0/1	0/5	0/6	1/34
1971-1972	—	0/1	0	0/1	0	0/2	0/2	3%
Total	0/4	0/5	0/3	0/4	0/3	0/19	0/24	
							0%	
Eremomela icteropygialis								
1968-1969	0	0	0/1	0/1	0	0/2	0/3	
1969-1970	0	0	0	0	0	0	0	
1970-1971	0/1	0	0	1/1	0/1	1/3	1/3	3/12
1971-1972	1/1	—	—	0	0	1/1	1/1	25%
Total	1/2	0	0/1	1/2	0/1	2/6	2/7	
							29%	
Combined hosts and years	2/16	0/27	1/12	10/56	0/10	13/121	13/143	16/206
	13%	0%	8%	18%	0%	11%	9%	8%
Both cuckoos, all hosts	12/41	0/30	—	—	—	23/149	23/171	30/245
	29%	0%				15%	13%	12%

[1] All-time, all South West Africa figures include post-1972 records from study areas.

[2] — = Not checked for breeding.

[3] X = No breeding records, occurs rarely, or absent.

[4] Figures in brackets refer only to the year indicated.

[5] First figure indicates the number of nests parasitized; the second figure represents the total number of breeding records.

Territory and Laying

After the first draft of this paper was written, a most important paper by Payne (1973) came to our hands, confirming and clarifying numerous aspects of cuckoo breeding biology for which we had only weak circumstantial evidence. Briefly, using histological and macroscopic analysis of numerous cuckoo ovaries, he concluded that eggs of *Chrysococcyx* and *Cuculus* in southern Africa are (1) laid on alternate days, with considerable voluntary control over actual time of deposition during the last 18 hours or so; (2) laid in clutches of one to five, usually three or four, with longer pauses of several days between clutches; (3) laid at an average rate of about two each week over a 10-or12-week breeding season, or 20 to 24 eggs per season.

Payne specifically states that these figures are modified by such factors as the number of available nests of hosts, and drought conditions. He also suggests that not all developing follicles ovulate. These conclusions fit extremely well with our field data.

Both Black and Klaas's Cuckoos, but more noticeably the latter, tend to shift "territorial foci" during the course of a season. Because we always knew the host for the Black Cuckoo, it was easier to relate available host pairs to a specific male cuckoo; but data from Klaas's Cuckoo, especially from Klein Spitskop, suggest a similar picture. The cuckoos call most actively in the vicinity of available host nests. Once a nest is past the stage when it can be parasitized, the calling focus shifts. When no more nests are available in an area, cuckoos tend not to be heard there any longer. If nests should again become available before the cuckoos leave for the north, calling resumes.

A female cuckoo parasitizing a relatively common host may thus ovulate a physiologically maximal clutch of four or five eggs and dispose of them during the rapid increase in nesting following the sudden appearance of favorable conditions. She then recuperates until a recurrence of favorable conditions induces a new cycle of renestings, second broods, etc. Such a situation might obtain in favored areas with Crimson-breasted Shrikes and Dusky Sunbirds. On the other hand, a cuckoo parasitizing an uncommon species, or one with a long nesting cycle (hence single-brooded), might use up only one or two eggs for each bout of nesting, and subsequently may have to range far to find additional hosts. Such a situation could well be the case with Klaas's Cuckoos parasitizing Yellow-bellied Bush Warblers.

In central South West Africa, the breeding season for a cuckoo probably lasts no more than eight weeks in an average year, and much less in the more arid parts. At Klein Spitskop, the maximum span of breeding of the female Klaas's Cuckoo we studied covered a period of eight weeks (Table 7), during which she could have laid about 16 eggs. If her territory contained 12 pairs of her host, the Dusky Sunbird, as indicated earlier, she would have a few eggs to spare. However, only a proportion of nests within her territory — never more than four in a season — were found parasitized. It seems that the theoretical and physiological possibilities are far from being fulfilled in practice, at least in our rather arid conditions, unless one assumes a horrendous rate of egg-loss.

Payne's (1973) postulated seasonal laying effort does, however, fit the estimates of territorial size in our cuckoos. Payne quotes similar-sized territories, worked out by careful observation, in the female European Cuckoo:

4 km of river frontage, or perhaps 40 hectares if appropriately converted. A Black Cuckoo laying 20 eggs in 15 nests of its shrike host would have to cover at least a 65-hectare area over 10 weeks, which is unlikely but not impossible, judging from our observations.

Incubation

With an incubation period of 13 to 14 days for the Black Cuckoo, and no more than 12 days for Klaas's Cuckoo, it is clear that the cuckoos hatch sooner than their hosts' young, sometimes by several days.

Eggs and Mimicry

The remarkable resemblance of color between cuckoo and host eggs demonstrated in this paper denotes intense selection for matching. The Black Cuckoo presents a fairly straightforward case, a climax situation of total specialization on one regional host.

Klaas's Cuckoo, on the other hand, exhibits perfectly color-matched eggs with at least two hosts. Strangely, the Crombec is apparently the least-parasitized host in central South West Africa (Table 9), in sharp contrast to the situation elsewhere (Jensen and Jensen, 1969). A possible explanation lies in the close resemblance of Dusky Sunbird eggs (Type 1) to Yellow-bellied Bush Warbler, and most Crombec, eggs in background and pattern and reasonably often in the color of markings (Table 6). If the Crombec is one of the ancestral hosts of Klaas's Cuckoo in the more mesic parts of southern Africa, we would expect it to have a well developed ability to discriminate against foreign eggs, thereby leading to the establishment of a gens with eggs closely matching those of the Crombec. With increasing discrimination, the cuckoo, arriving in the West and finding a new host similar in habits and nesting, but less discriminating, might switch to this easier victim, and perhaps temporarily reduce the numbers of the latter in the process. Its Crombec-mimic egg would be pre-adapted to the new host. Possibly because of decline in the warbler populations, or an increase in the number of cuckoos, another "host-hop" to the Dusky Sunbird might have taken place. Here again, a pre-adaptation of the egg to mimic the common egg pattern (Type 1) of the sunbird may have facilitated the switch. The above sketchy outline, modifiable in detail, illustrates the probable basic mechanism.

The explanation of gentes with different eggs evolving side by side is only a step or two more complex, although the South West African Pririt Batis gens probably originated by immigration of cuckoos that already parasitized the *Batis* genus in adjacent regions, rather than *de novo*.

It is frequently stated that gentes are indistinguishable morphologically; at least in the glossy cuckoos (*Chrysococcyx*), this may not be the case. A greater degree of polymorphism in plumage color exists among females of this genus than in any other cuckoos (Payne, 1967). This variation has not been linked with specific gentes, but this is unsurprising, even in the common Didric Cuckoo. However, the fact that this variation is limited to females ties in with the W egg-color hypothesis (Jensen, 1966), which restricts egg-color genes to the female-confined W sex chromosome. Payne's (1967:368) alternative explanation that female polymorphism is due to selection for individual variability to confuse hosts seems unconvincing *per se*.

Relative Abundance

The relative abundance of these two cuckoos, where they occur in South West Africa, is not easily clarified. Klaas's Cuckoo is uncommon to rare even though it may have increased in numbers within the 100-year span of ornithological history in the country. Black Cuckoos are quite common in suitable habitat in South West Africa. Both these cuckoos and others, like the Didric, appear to occur in pockets of relative abundance not clearly related to numbers of hosts, food supply, or other habitat factors. Furthermore, these "pockets" of cuckoos seem to be remarkably well-adapted to the idiosyncrasies of the local host populations. For example, Klaas's Cuckoo(s) at Klein Spitskop laid eggs matching the most prevalent sunbird egg type at that locality (Type 1, in 13 out of 14 clutches whose egg-color was seen or inferred from previous records in the same territory). In all three nests with parasitized clutches from Klein Spitskop, the cuckoo laid in nests of matching egg type. In two other cases, the color of the hosts' eggs could not be ascertained. At Groot Spitskop, the only cuckoo egg recorded in a sunbird nest was with a Type 3 clutch, and the cuckoo's egg matched this very well (Plate II). The data from the other hosts are too few to provide evidence, except that some Black Cuckoo eggs were a better match to their hosts' clutch than were others; but variation among eggs of the Crimson-breasted Shrike certainly does not compare to that in Dusky Sunbirds.

On this admittedly tenuous basis, we suggest an hypothesis that has the virtue of becoming testable at some future date when sufficient precise data have been accumulated. The available meager information on egg-color inheritance (in poultry, see Hutt, 1949, and Somes, 1973) suggests that heritability is fairly high, at least for major genes. These are probably homologous in at least the higher bird orders because of the general genetic conservatism of birds (see Jensen and Jensen, 1971 for discussion and references, and Takagi and Sasaki, 1974). Field observations on the insectivorous passerines used as cuckoo hosts certainly support the notion that they occur in clans of uniform egg types. The polymorphism of eggs in colonial granivorous-insectivorous birds, like some ploceid hosts of the Didric, is rather different. Cuckoos, such as Klaas's, would tend to occur in pockets within their host's range, the populations originating largely by chance adoption of a clan by a cuckoo with particularly well-matched eggs. If the host's ability to discriminate evolved through prior cuckoo contact, cuckoos that could not match the eggs of that host clan would rapidly be eliminated from the area. Likewise, the descendants of successful cuckoos would be successful breeders within the bounds of the clan, but relatively, or even totally, unsuccessful outside it. It is thus possible to visualize pockets in which cuckoos may be successful, interspersed with areas where the same host is common, but its cuckoo parasite rare or absent because of temporary or permanent inability to match the egg types of the host in those areas. Thus, the greater the inter-clan variation of host eggs and accompanying discrimination by the host, the more irregular a cuckoo's distribution. This simple picture is, of course, greatly complicated in practice by the other limiting factors discussed, as well as by the phenomenon of host-switching, and the varying ability of actual and potential hosts to discriminate between their own eggs and those of the cuckoo. In essence, this hypothesis is merely an extension of the gens theory to the community level.

What additional evidence may be adduced in favor of this picture? Firstly, pocket-occurrence or abundance among African cuckoos seems to be characteristic of the two *Chrysococcyx* (Didric and Klaas's) best known as parasites of several hosts, with intra-host variation of eggs in most cases. Secondly, constancy to breeding locality would be expected to occur in the females at least; and two ringed Didric males have been recaptured on identical territories in subsequent seasons (M. K. Rowan, pers. commun.). Thirdly, one could expect, due to ordinary linkage, that some morphological differences in appearance of the birds themselves might result from intense egg selection, by an extension of the W hypothesis (see previous section) to the pocket concept. It remains to be shown whether the morphology of adult female cuckoos can be linked with egg type. This has not been possible so far at the gens level with the best-studied species, the European Cuckoo, but would probably be much easier in the sexually dimorphic *Chrysococcyx* species.

Summary

New data on the biology of Black and Klaas's Cuckoos and their hosts in central South West Africa, with particular reference to breeding, are presented and discussed. These cuckoos lay well-matched eggs in typical cuckoo fashion in at least three of their five local hosts' nests.

The Black Cuckoo confines its brood parasitism to the Crimson-breasted Shrike in central South West Africa. Its eggs are fully described and illustrated for the first time. Matching of the eggs in color and size is excellent. Data on territory, courtship, laying, incubation period, and development of the young show it to be a typical *Cuculus*. A hand-reared nestling was returned to the wild successfully ("rehabitated") and yielded information on post-fledging development and behavior.

Klaas's Cuckoo paratitizes at least four hosts in the area under discussion: a flycatcher, a sunbird, and two warblers. Klaas's Cuckoo eggs were all from one area on the edge of the Namib Desert, and were found in three color types, with the two first-mentioned hosts. Matching of the eggs was good to excellent in color but they were much larger than the eggs of the hosts Pririt Batis and Dusky Sunbird. Two classic gentes are described for the first time in Klaas's Cuckoo. Data on territory, laying, clutch size, incubation period, and development of the young parallel *Cuculus* in most respects.

The incident and overall parasitism frequencies for these cuckoos suggest that the host-parasite population balance may be a tenuous one. An hypothesis extending the gens system to the infra-species population (clan) level fits the data and casual observations, particularly for Klaas's Cuckoo and its hosts. Further testing is suggested by correlating plumage characters in females with egg type and host preference.

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Violet-green Swallow, *Tachycineta thalassina*. Painting by Don Radovich.

THE PLUMBEOUS HERON OF THE GALAPAGOS[1]

Barbara K. Snow

The Plumbeous Heron, *Butorides sundevalli,* lives along the shores of the Galapagos Archipelago. Its confined geographic range contrasts with that of the Striated Heron, *B. striatus,* a pantropical species occurring in Africa, South America, Australia, southern Asia, and Polynesia. The Green Heron, *B. virescens,* is the third member of this genus and inhabits North and Middle America.

Most birds endemic to the Galapagos Islands have diverged so greatly that comparison with their nearest supposed relatives on the American mainland becomes highly speculative. The Plumbeous Heron, however, has diverged relatively little from the two mainland species. The Plumbeous Heron differs in appearance from its two congeners in plumage color, being generally a dark and rather uniform lava-gray. Its beak is also considerably larger (Gifford, 1913). I have used Meyerriecks' (1960) account of the breeding behavior of the Green Heron on Long Island, New York as the basis for a comparison of the Plumbeous Heron with its mainland relatives.

While residing at the Charles Darwin Research Station at Academy Bay on the island of Santa Cruz (or Indefatigable Island) in the Galapagos Islands from February through December 1963, I gathered data on the behavior and ecology of the herons that held territories along the shore in the immediate vicinity of the research station, mist-netting and color-banding four of the adult birds and all the young produced in this area.

Habitat

In contrast to the two other species of *Butorides,* which mostly inhabit the fresh-water systems of continents and islands, the Plumbeous Heron procures most of its food on the open foreshore. Occasionally, it hunts among the mangrove stilts or uses them as a perch from which to fish; but as mangroves form only a very intermittent and narrow belt along the high water mark, they are probably not sufficiently extensive to form a major part of its habitat. The Galapagos Islands have no fresh-water drainage system available to herons, since all precipitation percolates down into the lava. Some saline lagoons exist close to the shore, and the herons use them for feeding.

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The Plumbeous Heron's dark gray plumage is probably related to its primary feeding habitat, the bare lava rocks of the foreshore, and helps to render the bird inconspicuous when fishing and crab-hunting. The dark plumage does not reduce the heron's conspicuousness at the nest, which is normally built in mangroves. The position of the nest is advertised, rather than concealed, by the bird's behavior; and there are probably no indigenous nest predators.

Plumages

The plumage of breeding Plumbeous Herons varies considerably. My observations were not continued long enough to show whether or not these differences represented variations between sexes, individual variation, or birds breeding as subadults.

The plumage, generally a uniform dark lava-gray, is paler down the center of the throat and neck and the plumes on the back. This was the plumage of Female 3 throughout the eleven months and also of birds Banded 4 and Banded 5, of which Banded 4 was also believed to be a female. There were also a number of unbanded birds in this plumage.

The other plumage worn by some breeding birds, while also mostly lava-gray, had the following features that are reminiscent of the plumage of the Striated Heron: a pale off-white area streaked with dark feathers down the center of the throat, neck, and upper breast, narrow brown edgings to the coverts, and sometimes a black crown and crest contrasting with the paler gray feathers of the rest of the head and neck. This plumage was worn by Male 1, by a bird ringed by R. Lévêque in 1961 or 1962, and also by two other unringed birds seen at nests with dark lava-gray mates. These observations suggested that females were darker than males. However, nine sexed specimens in the British Museum, all from islands to the north and west of Indefatigable, show the reverse situation with males generally darker than females. Ridgway (1897) described the plumages of two birds from James Island in which the male was considerably paler than the female, corresponding closely to the plumages of Male 1 and Female 3, as described above. He also described adult males with pale plumages from Hood, Abingdon, and Chatham Islands.

Male 1 acquired a dark glossy black crown and crest during the second half of May. This period marked the completion of molt and preceded the June nesting. This male lost his black crown by the end of August. I recorded two other birds with black crowns: a banded bird in juvenal plumage, which developed between mid-April and mid-May a black crown that reverted to pale gray by mid-July; and an unringed adult in June.

There is also a change of color in the unfeathered parts, the most conspicuous being a change of the legs from gray to bright reddish orange. I noted this in Male 1 (but not his mate) two to three weeks before his mate laid eggs in both June and October. The legs changed to gray again when the first eggs were laid. Periodically, part of the lores turns yellow, forming a narrow streak running from the eye toward the bill. This loral streak was noted in Male 1 and other birds with partial Striated Heron-type plumage. I did not see it in Female 3, Adults 4 and 5, or any other birds in the dark lava-gray plumage. Male 1 lost his yellow lores when the first egg was laid in both June and October and regained it soon after the chicks hatched.

Whereas the change in the color of the legs and lores occurred with each breeding, the evidence suggests that the glossy black cap appears only once a year, around May or June. In his study of the Green Heron, Meyerriecks (1960) noted that the crown assumes a gloss in the breeding season, this change being more marked in the male than the female, as was the brighter leg color assumed in the breeding season. This parallels the changes in the Plumbeous Heron.

I collected some data on the change from juvenal to adult plumage. A banded juvenile retained its juvenal plumage for six and one-half months; it was next seen when seven and one-half months old, still in juvenal plumage except for one or two lava-gray feathers on the crown and a few adult scapular plumes. It was still in this plumage when I saw it two weeks later. If this age for the first plumage change is typical and is extended to a juvenile trapped and marked after it was independent of its parents, then the juvenal plumage — except for the adult features of the gray crown and scapular plumes — is retained until at least 10 or 11 months.

What is probably the next plumage stage was seen in an unringed bird that apparently did not own a feeding territory, but fished persistently throughout the period of observation at the western end of Territory 1 (Figure 1). From here it was persistently driven away by Male 1. Its plumage differed from that of Male 1 in being generally paler gray, particularly on the underside which also had a much wider central area of buff streaked with dark brown. The edgings to the wing coverts were also wider and paler. The plumage is so close to that of the Striated Heron that Harris (1973) suggested that this heron is also resident and breeding in the Galapagos. While no detailed observations have been published on the breeding behavior of the Striated Heron, Curry-Lindahl (1971), who has observed many races of both the Green and Striated Herons, states that the ethological and ecological characters of these two species are very similar, indicating very close relationship.

My observations of the one individual that looked most like the Striated Heron indicated that it was a sub-adult conspecific with, and showing no behavioral differences from, the local population of Plumbeous Herons.

Territoriality

Individual Plumbeous Herons occupy more or less exclusive feeding territories along the shore line. Along the stretch of shore where I made most of my observations, four territories adjoined each other (Figure 1). The extent of each individual's territory was judged to be the area from which it chased off other herons. Furthermore, territorial owners call when they fly within their territories; intruders are silent.

The four territories in the main study area were occupied by four color-banded birds, all breeding adults. These territories are given the same

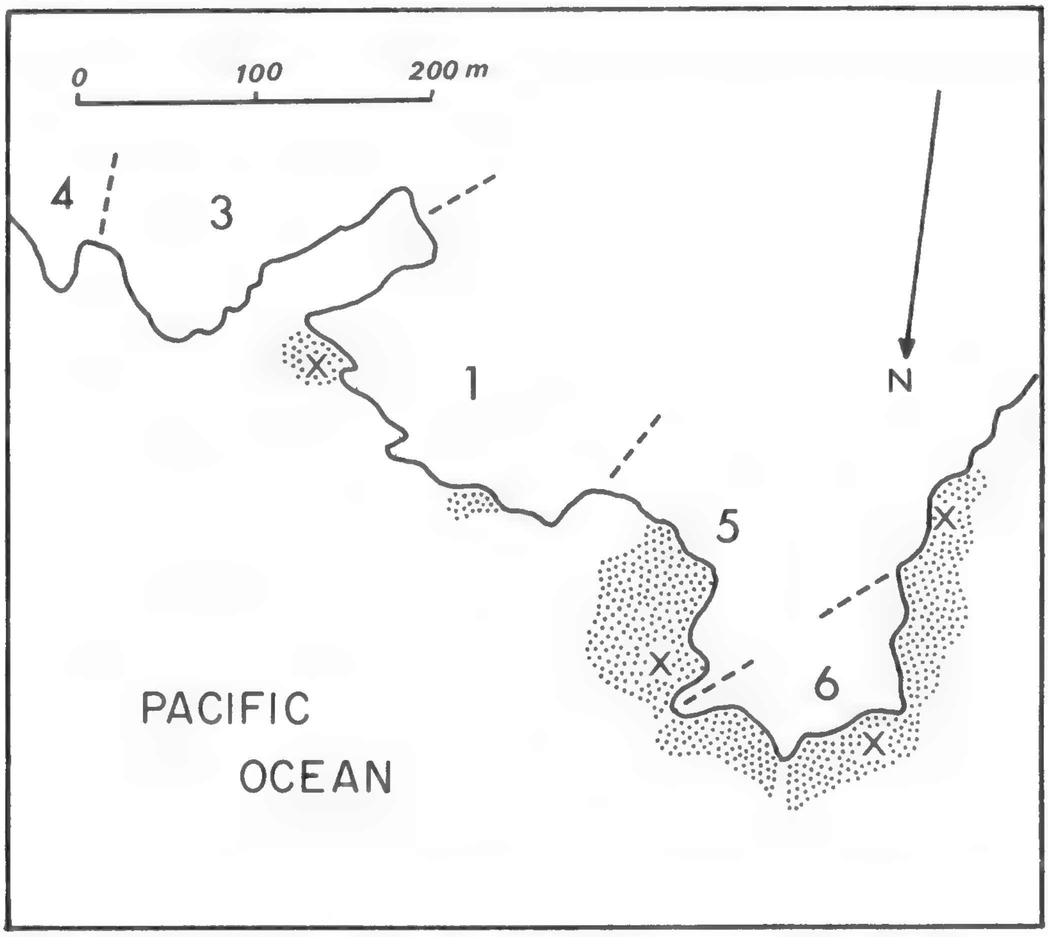

Figure 1. Map of the study area on Indefatigable Island showing territories of six Plumbeous Herons. Stippled areas indicate mangroves. An "X" marks nest-sites. The most westerly nest-site marked is that of Adult 4.

numbers as their owners. Male 1 had an unusually large feeding territory and was particularly aggressive. He fished in his own territory and, occasionally, also in the territory of his mate, Female 3, although he did not call in her territory. She tolerated him here, showing no signs of aggression. Once, Male 1 approached her in the aggressive hunched posture, but relaxed his aggressive posture when two or three yards from her, turned away, and continued to fish in her territory. Whenever Male 1 flew after an intruder, he stopped the chase and landed at the border of the adjacent territory of Adult 5 if chasing westward or, if flying eastward, at the border he shared in common with his mate (Figure 1).

Female 3 fished almost exclusively in her own territory but twice I saw her fishing in the territory of Adult 4. Once when she caught a crab (*Grapsus*) there, she flew with it in her bill to the center of her territory before eating it. During the nesting period, she fished in the immediate vicinity of the mangroves within Male 1's territory where she had a nest; but only once did I see Female 3 fishing to the west of the nest in her mate's territory and this was when he was incubating. I recorded one territorial encounter between the mated pair when the male drove his mate from the nest-site. The event took place 42 days after the accidental death of their half-grown chick and 43 days before the appearance of eggs in their next nest. Both birds were molting and the influence of the pair bond probably was at a minimum. Throughout the nesting period, the female treated the mangroves surrounding the nest-site as part of her territory and called as she landed there.

The fishing territory of Adult 4 contained no mangroves, but it probably served adequately as a feeding territory, since I at no time recorded this bird fishing in another heron's territory. Its nest, however, was nearly half a mile to the west in the extensive mangroves that surrounded an inlet where fresh water seeped into the sea. The fact that Female 3 nested outside its fishing territory suggests that Adult 4 also was a female.

The fishing territory of Adult 5, while it adjoined its nest-site, was evidently inadequate as a feeding territory; for 12 of the 24 fishing records for this bird were in other herons' territories, mostly Territory 1, but also Territories 3 and 4; and twice I recorded it fishing three-quarters of a mile to the east at a saline lagoon. In all these terirtories, it behaved as a trespassing bird, never calling and always flying away at the owner's aggressive approach.

In addition to these four birds, I recorded a bird ringed previously by R. Lévêque in 1961 or 1962, fishing frequently in Territories 1 and 5. This heron had no established territory in the study area. For a short period in June, when Male 1 was incubating, it defended the western end of Male 1's territory against other herons, but was driven off by Male 1 when the latter was not on the nest.

Food and Fishing Techniques

Food

Along the foreshore — that area of the shore between high and low water mark — I watched Plumbeous Herons capture 176 prey items, and found one pellet containing the hard remains of two crabs (*Grapsus grapsus*) and two prawns.

The different kinds of prey are shown in Table 1. These figures do not give a true indication of the relative importance of the different foods, for nearly all the prawns caught were very small ones that live in shallow pools. The eight large prawns were caught in pools only exposed at spring low water. Crabs and fish must make up the main bulk of the food. Of the four species of crabs caught, *Grapsus grapsus* was the biggest. Nearly all had a carapace width of one to two inches, the largest being about two and one-half inches. The three other species of crabs caught were all small with carapace widths of less than half an inch. Most of the fish caught were between one and one-half and two inches long; some were up to three inches. Most were bottom-living fish with cryptic coloration; others were free-swimming. Herons caught 92 percent of their fish prey and almost all of the prawns between half tide and low water.

Feeding Behavior

When catching fish, the Plumbeous Heron most commonly crouches motionless on the gray lava rocks at the edge of rock pools and thrusts its head and neck forward at an oblique angle into the water. In sheltered sandy areas, free-swimming fish are sometimes caught by standing in shallow water as the tide comes in.

The only pool in the study area a few feet below high tide mark was in the territory of Adult 5. As the tide left this pool large numbers of small prawns leapt out of the water at its outlet stream, probably in order to avoid being swept out of the pool. Adult 5 stationed itself at the outlet at the precise moment when the water began to leave the pool, often catching prawns at the rate of three to eight in five minutes. Adult 5 once used the same technique as the rising tide re-entered the pool and the prawns again began to leap. Other herons fishing for prawns lower down the beach used the same technique as the tide entered or left pools.

Both the prawn- and fish-catching are "stand and wait" techniques as described for the Green Heron by Meyerriecks (1960). The Plumbeous Heron, while poised motionless, often holds its body at an angle of about 45 degrees with its bill 6 to 12 inches above the water and the tail pointing skyward (Figure 2a). At times, it crouches so low that the bird's ventral surface is pressed against the rocks.

Crab-catching techniques were diverse, but all involved stalking, or walking or darting forward, described by Meyerriecks (1960) as the "wade or walk slowly" techniques.

The crab *Grapsus grapsus* is the most common prey of the Plumbeous Heron. This crab, when pursued by a predator, does not hide beneath rocks but scrambles rapidly away. It never takes shelter in the sea because it is preyed upon by two aquatic animals, the moray eel *(Cirrhitus rivulatus)* and an octopus (Kramer, 1964). The latter, by extending an arm, will even capture a crab that is on a rock close to the water. Much of the crab's feeding is done at the water's edge where the rocks are wet.

The Plumbeous Heron usually hunts *Grapsus* among the boulders around the high water-mark. To do so, the heron walks forward, crouching very low so that it is not visible to the crab until it emerges from behind a boulder and dashes toward its prey. At times, it stalks very slowly in full view of the crabs and then suddenly darts toward them. The heron also exploits the crab's reluctance to enter the water and sometimes maneuvers it onto a rock jutting out and darts to catch it as it hesitates at the water's edge. When the tide advances with sizable waves breaking over the rocks, a *Grapsus* occasionally becomes marooned on a rock with waves all around it, a situation of which the heron successfully takes advantage. Most individual crabs are very wary of the heron and, when aware of the latter's presence, keep a distance of three feet or more between themselves and a stalking heron. Large crabs, with a carapace of three inches or more, do not move at the approach of the herons; and the herons make no attempt to catch the crabs.

Although the time required for a heron to catch a *Grapsus* varies with conditions, the capture is often a slow process. Male 1, for instance, took 40 minutes to catch one *Grapsus* while traversing 35 yards of rocky foreshore where the crabs had concentrated shortly after high tide.

The small crabs, which include *Pachygrapsus* and *Uca helleri,* were caught among, or on, the stilt roots of mangroves when the tide first dropped and left the roots exposed. Occasionally a *Grapsus* was also caught here. Most crab-catching took place three hours either side of high tide — 68 percent of the 25 catches for which I recorded the tidal condition.

The drive to hunt prey appeared at times to be independent of hunger. I saw two different adults each capture a two-inch *Grapsus* and the rock fish *Dialommus fuscus* and, after holding them for a few seconds, deliberately let them go again.

Table 1

Prey Observed Caught by the Plumbeous Heron

Prey	*Number caught*
PRAWNS	
Under 10 mm	102
50 mm or over	8
Total	110
CRABS	
Grapsus grapsus	25
Pachygrapsus sp.	4
Uca helleri	2
Uca galaragensis	2
Small unidentified crabs from mangrove stilts	5
Total	38
FISH	
Dialommus fuscus (*Blennidae*)	6
Other bottom-dwelling fish (Blennidae, Gobidae, and others)	9
Silvery-sided free-swimming fish	5
Total	26
ISOPODS	2

I did not observe herons drinking sea water but once saw one 25 yards inland drinking at a brackish pool.

Even this brief study of the Plumbeous Heron's hunting and fishing techniques indicate how much success depends on the bird's knowledge of the behavior of its prey at different tide levels and in all the slightly different situations in which it may hunt for them in its territory.

Plumbeous Herons seize small prey crosswise a few millimeters from the tip of the bill and then immediately toss them back into the throat with a slight head movement. That this is a learned skill was demonstrated by the occasionally unsuccessful efforts of juveniles to swallow prey they had caught. Larger fish are swallowed head first with a more pronounced head jerk. Twice I saw the fish *Dialommus fuscus* being washed in a pool before it was eaten. Once, an adult heron caught an eel-like fish that wrapped itself around the bird's beak. After unsuccessful attempts to toss the prey into its throat, the heron dropped it.

After catching an especially big *Grapsus,* a heron often walks to the water's edge to dismember it, probably because here it can most easily recapture the crab if it escapes, as occasionally happens. The heron first knocks the crab against a stone, usually causing some legs to fall off; the body is then eaten, followed by the dismembered legs. Sometimes a heron carries a large *Grapsus* straight into the shelter of the nearest mangroves and dismembers it there. This is undoubtedly to escape the robbing intentions of the Lava Gull, *Larus fuliginosus* (Snow and Snow, 1969). The largest *Grapsus* that I saw a heron catch and eat was two and one-half inches across the carapace. The heron took its prey to the water's edge and there incapacitated it by passing it through the bill, exerting enough pressure to crush the carapace. The crab was then taken under the mangroves and dismembered.

Vocal Behavior

Aggressive Calls

I did not hear a vocal response to alarm in the Plumbeous Heron. This is probably because it appears to have no natural predators and is not afraid of humans.

The vocal repertoire consists of attack or hostile calls and an advertising call. Both calls are rendered by a heron in its own feeding territory or in the vicinity of its nest. A bird that trespasses onto the territory of another heron shows alarm behavior but invariably remains silent. Within its own feeding territory, a heron normally calls when it flies, and always when it flies at an intruder. This call consists of a succession of notes, *waark-waark-waark,* ending with a staccato cackle, *cuck-cuck-cuck . . .* as the bird lands. The *waark* is uttered with closed bill and the *cuck* with open bill. At times, only the *cuck* is given in flight. And sometimes a territory owner displaces an intruder by walking toward it, uttering this note. When flying from some distance into their nest, the marked pair sometimes made another call which sounded like *wa ha her ha her ha her . . .* This call also ended in the *cuck* as the bird landed.

The correlation between calling and position with respect to territory boundary was clearly demonstrated when, to delineate the territories of Female 3 and Adult 4, I gently drove them through their own territories and into the territory of their neighbor. The owner, while within its own territory, called during each short flight (about 10 yards) when I approached closely. However, when I drove a heron beyond its own territorial boundary, each flight was made in silence. The bird eventually doubled back into its own territory where it again called as it landed.

During change-overs at the nest, both birds uttered *waark* and *cuck* calls. A variation of the *cuck,* rendered with closed bill and sounding more mellow and reminiscent of the cluck of a chicken, was given near the nest, particularly by parents feeding a chick beginning to move about.

Both sexes gave what is probably a variation of the *waark* call, when defending the nest against an intruder. When this call, a continuous swearing, rasping *eeeark eeeark . . .*, is audible to its mate, the latter flies to the nest to assist in its defense, uttering the same call.

Advertising Calls

The Plumbeous Heron rarely uttered the advertising call. I heard only two individuals give this call. One was Male 1, which nested with the same female in the same mangroves in January, June, and October. By mid-December the change in the color of his soft parts indicated that he was again about to breed. After the Christmas holiday, repairs began on the jetty at the research station just beside the mangroves where this pair had nested during the previous 12 months. On the morning of 28 December, Male 1 delivered six advertising calls — a hoarse *quaark* given at two- to three-minute intervals — from a pile of rocks next to the only other patch of mangroves in his territory (Figure 1). He then re-entered these mangroves. Unfortunatley, observations ceased on this day so I did not learn if the pair subsequently nested here. It appeared that they were preparing to do so, having been displaced from their usual nesting site. The advertising call probably was associated with establishing a new nest-site in the part of the male's territory from which the female had formerly been driven away.

The other individual that uttered the advertising call was not banded. Its advertising call was a *kee-oo,* less hoarse than the call of Male 1 and more like that of the Green Heron, described by Meyerriecks (1960) as *skow.* When this bird uttered the call in May, it had extremely bright reddish orange legs, an indication that it was in breeding condition. While fishing one evening, it periodically uttered the call, and later, in the mangroves behind its fishing territory, this heron called *kee-oo* every 10 seconds for nearly 10 minutes. Two days later, the bird rendered the call intermittently when fishing. I did not hear it here again until 24 December, one month after a nest in this terirtory failed, at which time I heard a short series of advertising calls from the mangroves. Territory 6, which this bird occupied (Figure 1), was in the center of an inlet entirely fringed by mangroves that included a number of suitable nest-sites. The evidence on territories suggests that males are the most likely to own territories containing mangroves; possibly this bird's immediate neighbors were males. The need for advertising will be greater if the female does not own an adjacent feeding territory.

The migratory Green Heron frequently advertises vocally when it arrives at the breeding grounds, but the calls decrease sharply as pairing proceeds. There is a complete cessation of the call when the female is finally accepted and admitted to the nest (Meyerriecks, 1960). The rarity of the advertising call in the Plumbeous Heron therefore is not unexpected as the birds are resident, occupying the same feeding territories throughout the year, and may, as in the case of Male 1 and Female 3, nest in the same mangroves with the same mate three times in one year.

Alarm and Escape Behavior

As the Plumbeous Heron is not afraid of humans and has no indigenous mammalian predators, one rarely sees alarm and escape responses. Once an adult heron walked into the mangroves in response to a frigatebird (*Fregata* sp.) swooping down nearby after some of offal; but this was the only occasion when I noted an adult showing signs of alarm other than the response of a trespassing heron to the attack of a territorial bird. Usually, when the owner of a feeding territory notices an intruder and approaches either flying or walking in a hostile manner, the latter immediately flies off.

Occasionally, the intruder adopts a motionless Pointed Posture (Figure 2b) with all its feathers flattened, the head, neck, and body in line and oriented so that it points directly at the approaching bird. The intruder, extremely difficult to see in this position, may temporarily escape detection as the attacking bird flies past it. Adults and subadults, but not juveniles, adopt this posture. Possibly there is a slight hostile component in it as it was adopted most frequently by the subadult who trespassed very persistently on the westerly borders of Territory 1.

Juveniles occasionally assume an Upright Alarm Posture in which the crest may or may not be raised (Figure 2c). I once saw a subadult in this posture but never adults. Twice this display was assumed by birds landing in another bird's feeding territory and they were chased off by the owner in each instance. A juvenile, still dependent upon its parents for food, gave this display twice in its parents' feeding territory, once in response to the calling of some mockingbirds (*Nesomimus parvulus*), and once in response to my movements. On a single occasion, a juvenile trespassing in Territory 1 adopted this posture when a Lava Gull circled overhead. The posture appears to be similar to the alert posture showing the greatest escape tendency of the Green Heron (Meyerriecks, 1960, Figure 4).

Aggressive Behavior

The Plumbeous Heron defends a feeding territory throughout the year and nearly all the observed hostile behavior was associated with the maintenance of this territory. The hostile elements of the encounters between paired birds that take place within the mangroves where the nest was situated will be described separately. Except for one intrusion in the mangroves, all territorial encounters observed took place on the shore. I observed nothing in the nature of a fight nor any permanent changes in the territorial boundaries of the marked birds.

A heron trespassing in another's feeding territory is as silent and unobtrusive as possible. Although a heron on its territory is extremely vigilant and always seems to notice another heron that flies in, intruders frequently manage to fish in other birds' territories, probably by trespassing on foot.

If a territorial heron spots an intruder at a distance of about 100 yards or more, the owner flies toward it calling, and will normally land at, or near, the spot the intruder vacates. In flight, the defending heron frequently raises its crown feathers and scapulars and dangles its legs, actions characteristic of several flight displays of the Green Heron (Meyerriecks, 1960). As it approaches, it renders the *waark-waark-waark* call. If the intruder is less than 100 yards away, the attacking heron walks toward it in a hunched posture (Figure 2d) with scapular plumes and the feathers of the crown, neck, and breast raised, the tail rapidly flicking downwards, and giving a *cuck-cuck-cuck* call. When no intruders are visible and a heron flies from one part of its territory to another, it calls for the last few yards of its flight and lands in a hunched aggressive posture, but often without the crest and plumes raised.

The hunched aggressive posture is similar to the Forward Display of the Green Heron (Meyerriecks, 1960). Although the display takes place in trees near the nest-site and is usually stationary, it can also occur when stalking toward an opponent.

Only three times during the 11 months of observation did I record an adult heron with its neck extended upwards. This posture, although like the Upward Alarm Posture (Figure 2c), differed in that the neck feathers were all raised giving the bird a stiff, thick-necked appearance. Twice, Male 1 assumed this posture when an intruding subadult walked behind a boulder. The upright posture obviously gave the territory holder a better view than the hunched posture. On the third occasion, Male 1, having just driven his mate from a point where their two territories met, flew to the center of his feeding territory and assumed this position, then flew around his territory and again landed in this posture. No intruder had been observed in the territory.

The posture appeared to be primarily a hostile display, although there may have been some conflict between sexual and aggressive tendencies in the last-mentioned incident. It shows similarities with the Stiff-necked Upright Display of the Green Heron, which Meyerriecks (1960) describes as a rare threat display in which attack, escape, and sexual tendencies are in conflict.

Tail-flicking

A heron in its territory, or trespassing in a neighboring one, will give an occasional downward Tail-flick as it walks over the rocks. If it is stalking

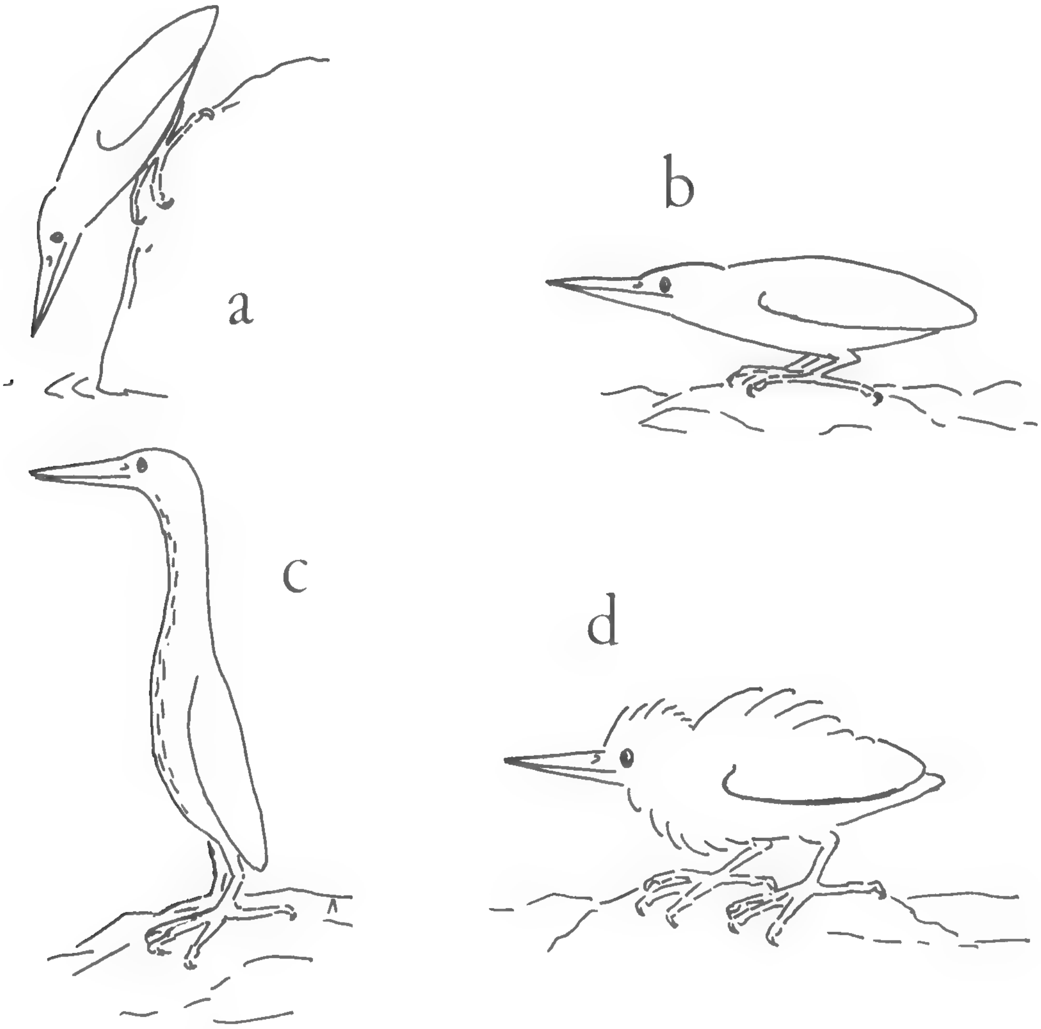

Figure 2. Several postures and displays of the Plumbeous Heron: A, Crouch-and-wait fishing posture; B, Pointed-posture of trespassing bird; C, Upright alarm posture; D, Hunched aggressive posture.

crabs, the frequency of Tail-flicks is greatly reduced. A territorial owner flicks its tail rapidly when walking in the hunched posture toward an intruder and also when it first lands after displacing an intruder. Occasionally, a heron hunting crabs runs quite fast in and out among the boulders. When doing so, it raises its crest and flicks its tail every half-second. The heron always flicks its tail downward and back to the horizontal position.

Nest Defense

The Plumbeous Heron defends its nest against a human intruder. I saw no other intruder, or potential predator, approach a nest.

Initially, when I was some distance off, the bird on the nest looked out over the side directly at me and slightly jerked or quivered its head; as I came closer, it assumed a hunched posture with all its feathers erected and its wings spread and held away from the body. From this position the bird shot its neck forward and opened its bill. With the neck fully extended, the head vibrated and a rasping *eeeark* was uttered. If the mate of the heron on the nest was within hearing distance, it returned, crouched on or near the nest, and displayed in like manner at the intruder.

In most respects, this display is similar to the Full Forward Display of the Green Heron (Meyerriecks, 1960), except that I did not observe Tail-flicking in the Plumbeous Heron; this could have been an omission of observation. In the Green Heron, this display is performed in a greater variety of contexts than I observed for the Plumbeous Heron. The display is also very similar and probably homologous to the Threat-gape Display of the Shag, *Phalacrocorax aristotelis* (Snow, 1963), the Flightless Cormorant, *Nannopterum harrisi* (Snow, 1966), and many other members of the family Phalacrocoracidae (van Tets, 1965).

Behavior of Pairs at the Nest

Except for the very few occasions when the advertising call was heard, I observed none of the early stages of courtship.

I saw copulation once in the banded pair. At 09:30 the female returned to the nest where the male was covering the first egg laid that morning. After the changeover, the male stood beside the nest preening for a minute, then went back onto the nest and mounted the female. During copulation, the male just touched his bill to the rim of the nest and briefly flapped his wings. The female sat in the nest with outstretched neck. The incident was not accompanied by vocalizations, and lasted no more than a minute.

The fact that members of a pair defend separate fishing territories during the nesting period indicates the presence of an antagonistic element in their mutual relationship. This is manifested at the nest, where initially both sexes show hostile behavior.

A heron of either sex normally calls as it flies toward the nest and lands outside the mangroves uttering the *cuck* call. It climbs up to the nest in the hunched posture, with feathers and plumes erected. The incubating bird also utters the *cuck* call and assumes the hunched posture, either crouching or standing in the nest. When the approaching bird is within about three yards of the nest, both birds stop calling and cease the Forward Display. At this point the bird in the nest stops looking at its mate, and looks downward, inserts its bill into the rim of the nest, and makes small lateral head movements as if inserting a twig. The arriving bird, when it reaches the nest, makes the same movements in the nest rim near the bill of its mate. Sometimes a stick is picked up and re-inserted with this movement. A very similar lateral head movement termed Nest-quivering is made by the Shag (Snow, 1963) and the Flightless Cormorant (Snow, 1966).

At one nest relief that I observed, both birds extended their necks and made preening motions with a lateral head movement in the scapular plumes of their partners. Similar Feather-nibbling is described for the Green Heron (Meyerriecks, 1960).

Juvenile Behavior

The term "juvenile" here applies to birds that have left the nest and continue to be in juvenal plumage. I observed the behavior of four banded juveniles, three of which were ringed as nestlings and one just after it had left the nest.

Three of these juveniles were last seen in their parental territories at ages of 53, 53, and 54 days; the fourth, Juvenile D, stayed until 81 days, 23 days before its mother began to lay another clutch. Juveniles food-beg from their parents almost until the time of their departure. A juvenile aged 47 days was the oldest juvenile I recorded receiving food from its parents. While they remain in their parents' territories, juveniles do not wander far from the nesting area, which is where parents feed them. Judging from their desultory and frequently unsuccessful attempts at catching prey, juveniles obtain little food for themselves until the normal age of departure at about 53 days.

I first saw juveniles walking about on the shore and among the shallow silty pools below the mangroves at an age of 27 to 30 days. At this age they seize and mandibulate in the tips of their bills all sorts of inanimate, usually elongated, objects such as rolled up leaves, leaf stipules, and bits of root. They also pick up and put down again hermit crabs lodged in the shells of gastropods. This exploratory mandibulating of inedible objects continues until they are at least 40 days old. I first saw juveniles catch prey between 33 and 35 days. One juvenile caught a small prawn and held it for about 20 seconds in the tip of its bill before swallowing it; another caught a small starfish that wrapped itself around the tip of the heron's bill where it remained for 20 minutes without either escaping or being swallowed. Four days later the same juvenile caught a small species of crab (*Pachygrapsus* sp.) among the mangroves that, when caught, presses its legs tightly to its body so that it appears to have changed into a round pebble. The juvenile managed to swallow the first two crabs it caught, but it seemed unable to shift the next one from its bill tip to its throat. After picking it up and putting it down about twenty times, it abandoned the attempt. Early efforts by juveniles to catch *Grapsus grapsus* were invariably unsuccessful, for the young herons clumsily hopped and ran after the crabs instead of stalking them. Between the ages of 64 and 81 days, Juvenile D caught several species of crustaceans, including *Grapsus, Uca helleri, U. galapagensis,* and small prawns. Three juveniles flew voluntarily at ages 43, 46, and 51 days. Another juvenile had not been seen flying when last observed in its parents' territory at 54 days of age. This is not surprising in view of the fact that adults seldom fly within their territories, except when chasing off intruders or when flying back to the nest.

When 64 days old, Juvenile D showed incipient nest-building behavior, picking up a stick and carrying it to the beginnings of an unsuitably situated nest. The nest was almost certainly constructed by the juvenile and not its parents, which built a nest a few weeks later about 15 yards away. It also defended the nest at my approach by moving to a position just below it and calling with a softer, less staccato version of the adult's *cuck-cuck*. Except for the food-begging call, this was the only occasion when I heard a juvenile calling in its parents' territory.

I did not witness the expulsion of a juvenile from its parents' territory. Three of the juveniles were not seen again after their departure. A juvenile reared in Territory 5 (Figure 1), which it left at the end of April, I saw seven times during the next seven months at different points along the mile and a half of foreshore to the east. I saw it most frequently near a saline lagoon three-quarters of a mile away and never nearer than a quarter of a mile from its parental territory. It was always silent, furtive, and inconspicuous; but even so, adults frequently chased it off. I judged its fishing abilities, observed when it was 81 days old, equal to an adult's.

Breeding

Breeding Season

I found a total of seven nests with contents in the study area and one on the west side of Academy Bay. I recorded an additional breeding record in the study area from an observation of a parent feeding a juvenile. Nine nests with contents were found on islets to the north of Indefatigable. These breeding records, combined with those published by Lévêque (1964), indicate breeding throughout most, if not all, of the year (Table 2). Possibly there is less breeding activity from May to August, the "garua" season, when the weather is windier and cooler than in other months. One pair of banded herons bred three times during the year, with the following dates: 22 January, 6 June, and 9 October. Final observations on this pair, at the very end of December, suggested they were about to start breeding again. The male of the pair molted throughout April and May; the female molted from late March until early June. The nestling from the January nest died from an accident on 13 March and this may have influenced the onset of the parents' molt. One other marked adult also molted during March and April.

Nest Site

Twelve occupied, and eight old, nests were located in mangroves between 4 and 15 feet above the ground, with an average height of nine feet. Harris (1974) also found nests under rocks. The marked pair nested three times in the same clump of mangroves, twice using the same nest. A replacement for a nest from which the eggs were lost was built two yards away. The herons built their nests well-separated from one another and within a defended territory. On a small islet in the channel between Indefatigable and South Seymour, however, three occupied nests and six empty ones were found within a few yards of each other. The neighboring coast of Baltra lacks mangroves; thus, a shortage of nest-sites probably had forced the local herons to nest colonially.

TABLE 2

Breeding Season of the Lava Heron

Number of Clutches Started in Each Month[1]

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
5	7	3	2	3	2	1	0	5	8	4	7

[1] Data from this study and Lévêque, 1964.

Clutch Size and Egg Size

The Plumbeous Heron normally lays a clutch of two eggs, occasionally three. Two days separated the laying of eggs in a clutch. The average size of nine clutches was 2.2. This figure includes two clutches recorded by Lévêque (1964). This is a smaller clutch than that recorded for the Green Heron in Mexico, where Dickerman *et al.* (1969) recorded the average of 175 clutches at 2.75. Hellebrekers (in Dickerman *et al.*, 1969) recorded an average of 2.67 eggs in 68 clutches of the Striated Heron in Surinam.

I weighed and measured a few eggs. The eggs from a clutch of three weighed 15.5, 16.5 and 17.0 grams. Two clutches of two laid by the same marked female were the following sizes: the first egg measured 31.2 x 41.0 mm and weighed 22.0 gm; the second egg measured 31.0 x 40.2 mm and weighed 21.5 gm. Weights were taken after two days incubation. In the second clutch, the first egg measured 31 x 41 mm and weighed 20.5 gm; the second egg measured 30.5 x 40 mm and weighed 19.5 gm. Weights were taken after seven days of incubation. The last egg, reweighed at the time of pipping, had lost three grams during 18 days of incubation. Adjusting the third clutch for weight loss due to incubation, the average weight of the seven eggs was 19.2 gm, heavier than the eggs of the Green Heron in Mexico (197 eggs, average 17.1 gm) recorded by Dickerman *et al.* (1969) and of the same species in New York — 17.4 gm for 74 eggs (Meyerriecks, *in* Palmer, 1962).

Incubation Period

The length of the incubation period was recorded at one nest. The first egg hatched 22 days and the second egg 21 days after being laid (∓ one-half day). This closely matches the length of incubation of the Green Heron in Mexico, where the first eggs of each clutch hatched in 21 to 23 days (Dickerman *et al.*, 1969).

Nesting Success

I determined the success of five nests found during, or just after, laying. One clutch of three eggs was depredated halfway through incubation. Of the four remaining clutches, all eight eggs hatched and four young fledged, one from each nest.

Apparently two nestlings never fledge from the same nest because the older nestling, probably activated by hunger, prevents the younger from getting any food after its fifth day. This drop from two chicks to one I noted at six nests. Another three nests had single nestlings 13 days and older. Lévêque (1964) gives details of two nests, in each of which two nestlings hatched and single nestlings remained when 9 to 10 days old. Brosset (1963) likewise never saw more than one half-fledged young in a nest.

Nestlings

Changes in Weight

I recorded the development and increase in weight of the nestlings in two nests of the banded pair, and gathered some supplementary information on two other nests. In these four nests, the two eggs of each clutch hatched and the younger of the two nestlings, which hatched on consecutive days, died when eight or nine days old. These younger nestlings achieved their peak weight when four or five days old (Figure 3), and their subsequent development was retarded.

The eggs of the two nests under consideration were laid in June and October, and the development of the nestlings occurred mainly in July and November. The nestlings gained weight more rapidly in November than in July and the stages of physical development appeared sooner. This is possibly related to the fact that the June nesting was outside the main breeding season (Table 2) when presumably conditions are less favorable.

The death from starvation of the younger nestling when eight or nine days old, after both had shown an inability to maintain their increase in weight between four and six days, suggests that certain foods, most likely the large *Grapsus,* are unsuitable for small nestlings. Their combined weights at this age did not exceed 90 gm, as compared to a subsequent weight of about 200 gm attained by the surviving chick. Thus, it seems unlikely that the adults were unable to supply a sufficient bulk of food. Similarly, in some sea-birds that swallow their food whole without dismembering it, there is evidence that chicks die of starvation at a young age, such as the Red-footed Booby (*Sula sula*) with a single nestling and therefore no competition with nest-mates for food (Nelson, 1969), and the Shag with up to four young in the nest (Snow, 1960).

Feather Development

A newly hatched nestling is covered with down about 16 mm long on all the feather tracts. The down is dark gray above and pale gray below. The eyes are open and the upper mandible, with a small egg-tooth, is shorter than the lower mandible. The two mandibles become equal in length at the age of three to five days. The eye color, dark brown on hatching, changes to a dark khaki when the nestling is two or three days old and to a paler khaki when five days old.

The pinfeathers of the wing and body but not the head, neck, and tail appear on the ninth day, and the scapular feathers begin to break out of their sheaths by the 11th day followed on the 12th day by the feathers of all body tracts except the head. The flight feathers of the wings, or remiges, emerge from their sheaths on the 13th day. These stages of development apply to the November nestling whose weight was 20 to 50 gm greater than that of the July nestling and whose stages of plumage development were two or three days earlier.

After 16 days of age, the nestlings escaped capture by clambering away among the mangroves, and I could no longer record the details of development. However, I estimated the contour feathers to be three-quarters out of their sheaths at the age of 23 days. At 27 days, when the nestling left the nest, it was well feathered, but with down still attached to the tips of the feathers on the head and thighs; the tail was short. In another week the tail was full grown but down remained on the head for an additional 10 days.

Development of Locomotion and Behavior

For the first three days, the nestling's only movement is to raise and sway its head with open bill when food-begging. When four to five days old, a nestling resists being taken from the nest by clinging to the nest. When five to six days old, it can stand in a semi-upright position by balancing on its tarsi. In all the nests studied in detail, the older nestling, when eight days old, started attacking its younger sibling. It is evident from the weights (Figure 3), however, that competition for food started sooner, since the growth curve of the older nestling showed a temporary drop about the sixth day and the two younger nestlings reached their peak weights on the fourth and fifth days. The older nestling, when pecking the younger, raised itself up as high as possible, drew its head back and struck forward and down at the head of its sibling. If the younger nestling re-

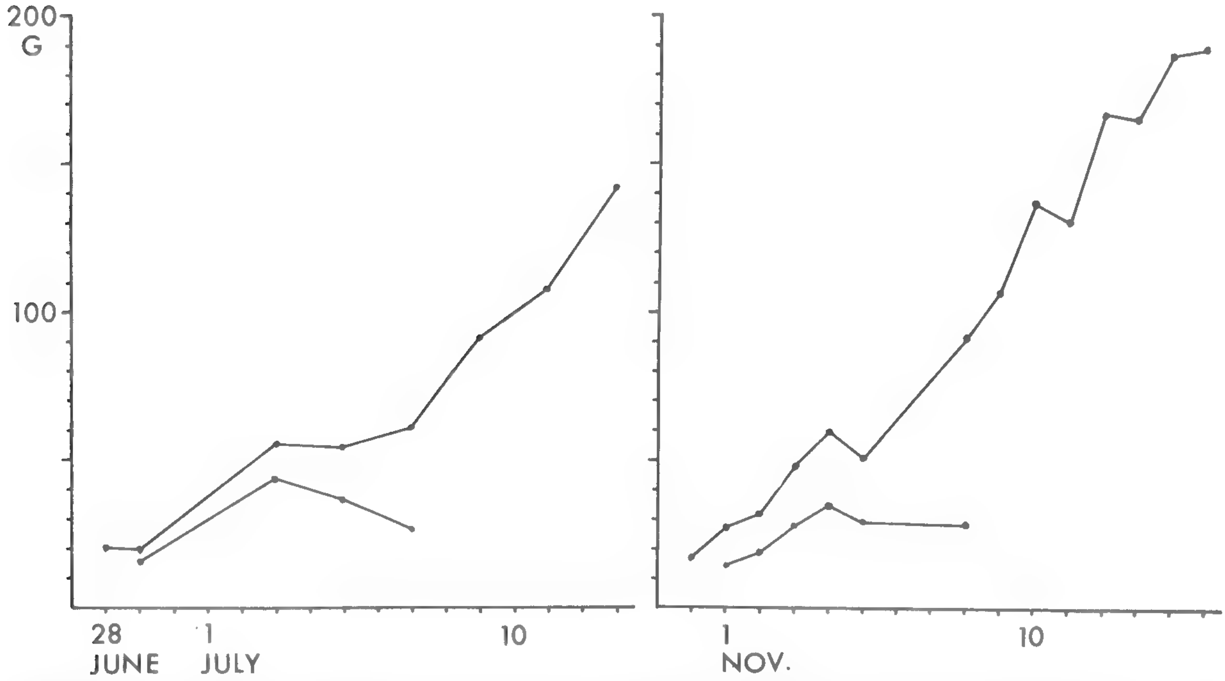

Figure 3. Graph showing the daily weight changes from the day of hatching of two broods The younger nestling in each brood died soon after the final weighing.

mained quiescent in the nest, it normally was not attacked. The aggressive behavior usually resumed, however, whenever the younger nestling raised its head. Most of the blows were directed at the back of the head, which became bruised and raw. Two days after the attacks began, the younger nestlings died. In the cases I observed, death apparently resulted from starvation rather than from the damage inflicted; but without the evidence from weighing, which suggested that the aggressive behavior was triggered by hunger, I would have interpreted the behavior as unprovoked attack, causing fratricide.

At eight days of age, the older nestling starts to defend the nest with an imperfect rendering of the adult's Full Forward Display accompanied by a high thin version of the *eeark* call. It also pecks at an approaching hand. At this stage, or a day earlier, nestlings cling with their wings and chin, as well as their feet, so that they are extremely difficult to lower into a bag for weighing. At 13 days, a nestling that lost its balance supported itself hanging upside down by means of its chin, wings, and feet, and nestlings may well be able to do so at an earlier age, but their ability was not tested. Around 12 to 13 days, when nestlings first try to escape capture by walking away from the nest along a branch, they perform the downward Tail-flick with an unfeathered stump of a tail.

Between 12 and 15 days, the nestlings were left alone, but one parent usually fed nearby and returned to the nest when it heard the nestling defending it at my approach. At 18 days of age, nestlings clambered through the mangroves away from the nest but returned to the nest and were fed there for an additional eight or nine days. At 23 days, when wandering about in the mangroves they pecked and pulled at twigs and leaves and occasionally their own legs and feet. Sometimes they became motionless, gazing in a fixed manner at an object, then darted the head and neck out to seize it in the manner of a fishing adult. The nestlings under observation finally left the nest when 27 to 30 days old and climbed down to the ground beneath the mangroves. They remained within the shelter of the mangroves, or near them, for several days. There was no evidence that nestlings at these ages had attempted to fly, nor had I seen them engage in wing-flapping exercises.

Discussion

If the ancestors of the Plumbeous Heron first colonized the Galapagos Islands relatively soon after their volcanic emergence, the habitat available for hunting would probably have been only volcanic rock descending precipitously into the sea. Of the main prey now taken by the Lava Heron, only the crab *Grapsus grapsus* could flourish in such a habitat. The relatively recent islands Wenman and Culpepper, in the northern part of the archipelago, possibly show something approaching these conditions. On these two islands, *Grapsus* is abundant and the heron is present although no information is available on its breeding status. Evolutionary changes that enabled the colonizers to be more successful at preying on the crabs must have had a high survival value. Such changes probably included the acquisition of a darker plumage matching the lava background, and an increase in the size of the bill, which averages six to seven mm longer and is correspondingly heavier than the bill of the Striated Heron in South America.

As the Galapagos Islands matured, they developed a much more varied coastal habitat, with inlets and bays partially filled with sand and detritus and often fringed with mangroves; the coast developed more shelving, with tidal pools, and, where beaches have been substantially built up, quite large areas of saline lagoon have formed behind them, as at James Bay and behind Caleta Black on Albermarle.

If the assumption is correct that the Plumbeous Heron's lava-gray plumage evolved to facilitate hunting among lava rocks, the dark plumage should no longer have as strong a selective advantage with the evolution of a more varied coastline; the advantage will now vary from locality to locality. This could explain the variability in plumage, from the typical dark gray form to the streaked and paler form resembling the Striated Heron, and it could also account for the different forms being more common in some localities than in others (Harris, 1973).

The Striated Heron breeds both in small colonies, usually in mangrove swamps (Bannerman, 1930; Clancey, 1964; Haverschmidt, 1968), and solitarily beside inland waters such as lakes, rivers, or creeks (Jackson, 1938). The Green Heron is also both a solitary and colonial nester (Palmer, 1962). Some individuals, nesting in a large colony on Long Island, also defend separate feeding territories (Meyerriecks, *in* Palmer, 1962). In its wintering quarters in Florida, this species feeds in the mangrove zone and is highly territorial (Meyerriecks, pers. commun.). Birds nesting solitarily probably defend the surrounding area as a feeding territory. This flexibility of nesting behavior suggests that no fundamental change in behavior was necessary when the ancestor of the Plumbeous Heron colonized the Galapagos Islands. Many factors that may favor colonial breeding in other populations would not apply in the Galapagos, such as the advantage of nesting on off-shore islands or in swampy areas inaccessible to mammalian predators, and the advantages of being near large areas of freshwater swamp that have a seasonal super-abundance of food.

The coastal climate of the Galapagos is relatively uniform and the heron's littoral food sources did not show any obvious seasonal fluctuations. Judging from the apparent inability of the Plumbeous Heron to rear more than one nestling at a time, food is probably never very abundant. The permanent occupation of linear feeding territories that can be effectively defended, and that also may contain the nest, might be essential for the successful rearing of a nestling.

Compared to the Green Heron, the Plumbeous Heron has fewer calls, displays, and escape responses, probably due to a sedentary existence and lack of predators. It has no call analogous to the *skyow* or *skeow* which the Green Heron renders when it flies from a human intruder or a Marsh Hawk, *Circus cyaneus* (Meyerriecks, 1960). All the escape flights of the Plumbeous Heron that I saw were away from conspecifics, where silence is advantageous if the fleeing bird lands in another heron's territory.

Another alarm response missing in the Plumbeous Heron is the Bittern Stance, a motionless upright posture with bill pointing skywards, which enhances concealment. The Green Heron gives this display both at the nest and while feeding. On the foreshore where the Plumbeous Heron feeds, the Bittern Stance would be useless as a means of concealment; at the nest, where it could possibly serve this purpose, the species has no indigenous enemies.

The sexual displays common in the Green Heron but not seen in the Plumbeous Heron are the Snap Display, Stretch Display and its variations, Flying Around, and Circle Flight Display. More intensive observation might show that these displays occur very rarely in the Plumbeous Heron, as does the advertising call. Probably, the hostile behavior with which it defends its feeding territory advertises its availability as a mate. Furthermore, the sedentariness of this heron makes advertising less necessary.

A Plumbeous Heron that owns an adequate feeding territory seldom flies. It does so only to chase off an intruder; one within 10 yards or so it chases on foot. A heron also flies when returning to the nest after fishing some distance away. If a heron fishes within approximately 20 yards of the nest, it walks back and climbs up the mangrove to it. A territory owner, if not engaged in breeding, spends many hours in its territory "on foot," walking out to the area where it hunts and then to a large rock or a clump of mangroves where it normally rests and preens. Where a species does not require flight to feed efficiently, reach its nest-site, or escape from danger, it must be potentially susceptible to the evolution of flightlessness.

Compared to other *Butorides* species, the Plumbeous Heron shows a reduction in clutch size and an increase in egg size; but the greatest decrease in reproductive output occurs during fledging and results from the behavior of the older chick. This behavior with the subsequent loss of younger nestlings has not been reported for other species of *Butorides* (Cowles, 1939; Meyerriecks, *in* Palmer, 1962). In Trinidad, we found nests of Striated Herons containing three and four three-quarter-grown young. Within the Ardeidae, loss from starvation of younger members of a brood has been reported in the Cattle Egret, *Ardeola ibis* (Blaker, 1969), and in the Gray Heron *Ardea cinerea* (Owen, 1960). In these species, some fighting and pecking occurs between siblings, but nothing similar to the persistent attacks of the older Plumbeous Heron chick on its nest mate.

Summary

An eleven-months study of a small, partially color-ringed population of Plumbeous Herons (*Butorides sundevalli*) in the Galapagos Islands showed that breeding adults are highly territorial throughout the year. Each member of a pair defends a separate section of the foreshore as a feeding territory, which may also be the site of the nest. Immature birds lack feeding territories and are continually driven off by territory-holders. The Plumbeous Heron feeds largely on fish and crabs, particularly *Grapsus grapsus,* and also prawns.

Present data show breeding in all months of the year except August, with 77 percent of the nests active from October to February. A marked pair bred together three times in the year, the male showing a change in the color of its soft parts at each nesting.

The differences in the behavior of the Plumbeous Heron compared with the Green Heron (*Butorides virescens*), intensively studied by Meyerriecks (1960), center around the Plumbeous Heron's entirely sedentary existence, permanent pair-bonds, and lack of enemies. Consequently, its advertising displays are rare or missing and its calls are mainly related to the defense of its feeding territory against conspecifics. Alarm and escape behavior were seen as responses of a trespasser to the hostile attacks of a territorial heron. I recorded no alarm call.

Compared to other species of *Butorides,* the Plumbeous Heron has a slightly smaller clutch and slightly larger eggs. While predation at the nest is negligible, only the oldest chick survives. When the older chick is eight days old, it starts attacking its sibling, younger by one day. The younger chick, unable to get any food, dies two days later. The remaining chick leaves the nest when about 27 days old but remains within the territory of the parents and is fed by them for at least 26 days longer.

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OLD FORGE, WINGRAVE, AYLESBURY, BUCKINGHAMSHIRE, ENGLAND

BREEDING BIOLOGY OF SWALLOW-TAILED KITES IN FLORIDA

NOEL F. R. SNYDER

Photographs by the author

The Swallow-tailed Kite (*Elanoides forficatus*) is still common and conspicuous in parts of its formerly extensive range. Even so, it has received relatively little study. Bent (1938) reviewed a number of short reports on the species, and more recently, Skutch (1965) presented his notes on these raptors in Costa Rica. In addition, Sutton (1955) and Wright *et al.* (1970, 1971, and 1972) have published popular accounts of the nesting of the species in Florida. Despite these reports, many basic facts have remained undescribed, such as the roles of sexes through the nesting cycle, the length of the incubation period, and the diversity and function of vocalizations. This paper, based on a study of the nesting biology of a small population of Swallow-tailed Kites in a mangrove swamp of southwestern Florida, fills some of the gaps.

Methods

The study area was an extensive swamp of red, white, black, and buttonwood mangroves (*Rhizophora mangle, Laguncularia racemosa, Avicennia nitida,* and *Conocarpus erectus*) near the northwestern boundary of Everglades National Park (Figure 1). Within the swamp, the kites confined their nesting activities to a zone of relatively tall black mangroves ranging to about 15 meters in height. The nearest edges of the swamp lay more than one kilometer to the southwest and approximately nine kilometers to the northeast of the nesting grove. Access to the area was by boat.

The water in the mangroves varied from salty to fresh, the salinity depending on location and season. A sample taken in May from a backwater near one of the nests of 1969 contained approximately 40 parts salt per thousand, a greater concentration than in seawater. The presence of hylid frogs in the mangroves can probably be attributed to a considerable freshening of the waters during the summer rainy season.

The nesting area is known to have been occupied by kites in 1967, and from 1969 through 1972; but we made only brief observations in 1967, 1970, and 1971, and none in 1968. In 1969 we observed two nests closely from blinds during the incubation and nestling periods. Both nests were successful, fledging one and two young, respectively. In 1972 we studied from a blind a single nest beginning with incubation and ending with the nest's failure part way into the nestling period. Additional notes were made on the above nesting pairs during the nest-building period and on other pairs of kites in nearby areas at various stages of the nesting cycle.

The nests of the kites we studied were placed at heights of eight to twelve meters near the tops of black mangroves that stood apart from other mangroves, allowing unobstructed approach by air (Figure 2). The two nests of 1969 were located about 200 meters apart, and the 1972 nest was about 20 meters from one of the former. The nest occupied in 1972 may have represented a subsequent nesting of adults studied in 1969.

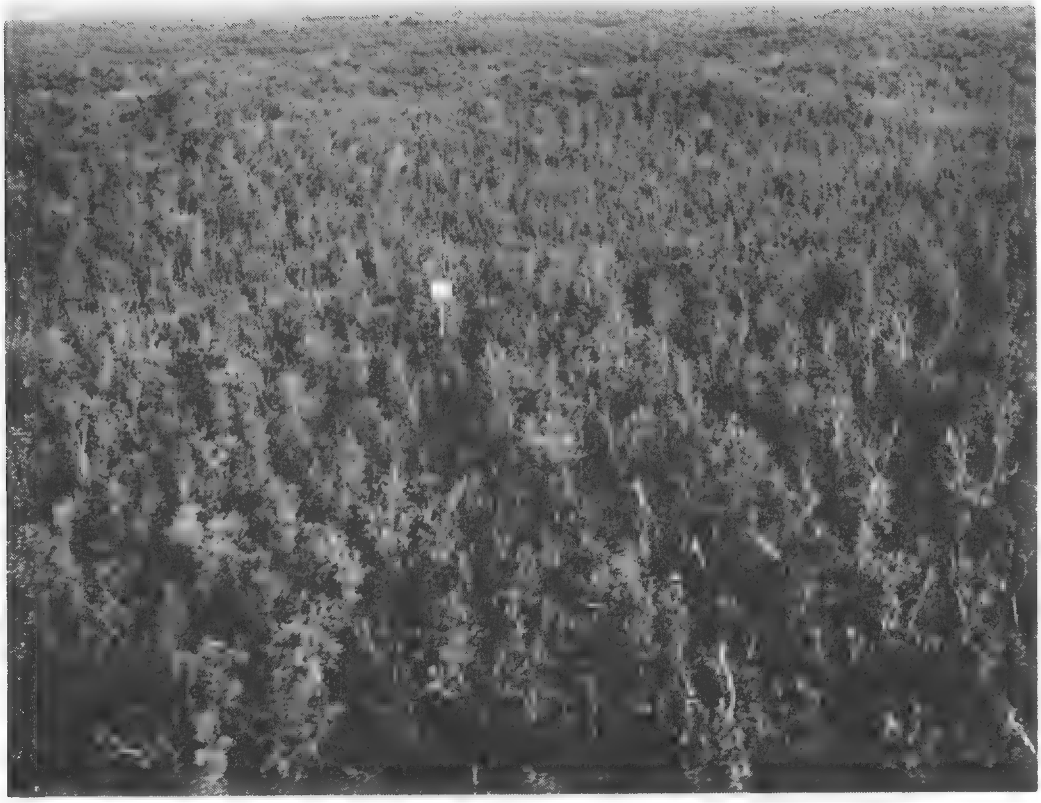


Figure 1. Aerial view of the nesting area of Swallow-tailed Kites in southwestern Florida. A 10-meter-high tower and blind (*top center*) overlooks the active nest of 1972. Dominant vegetation is black mangrove (*Avicennia nitida*).

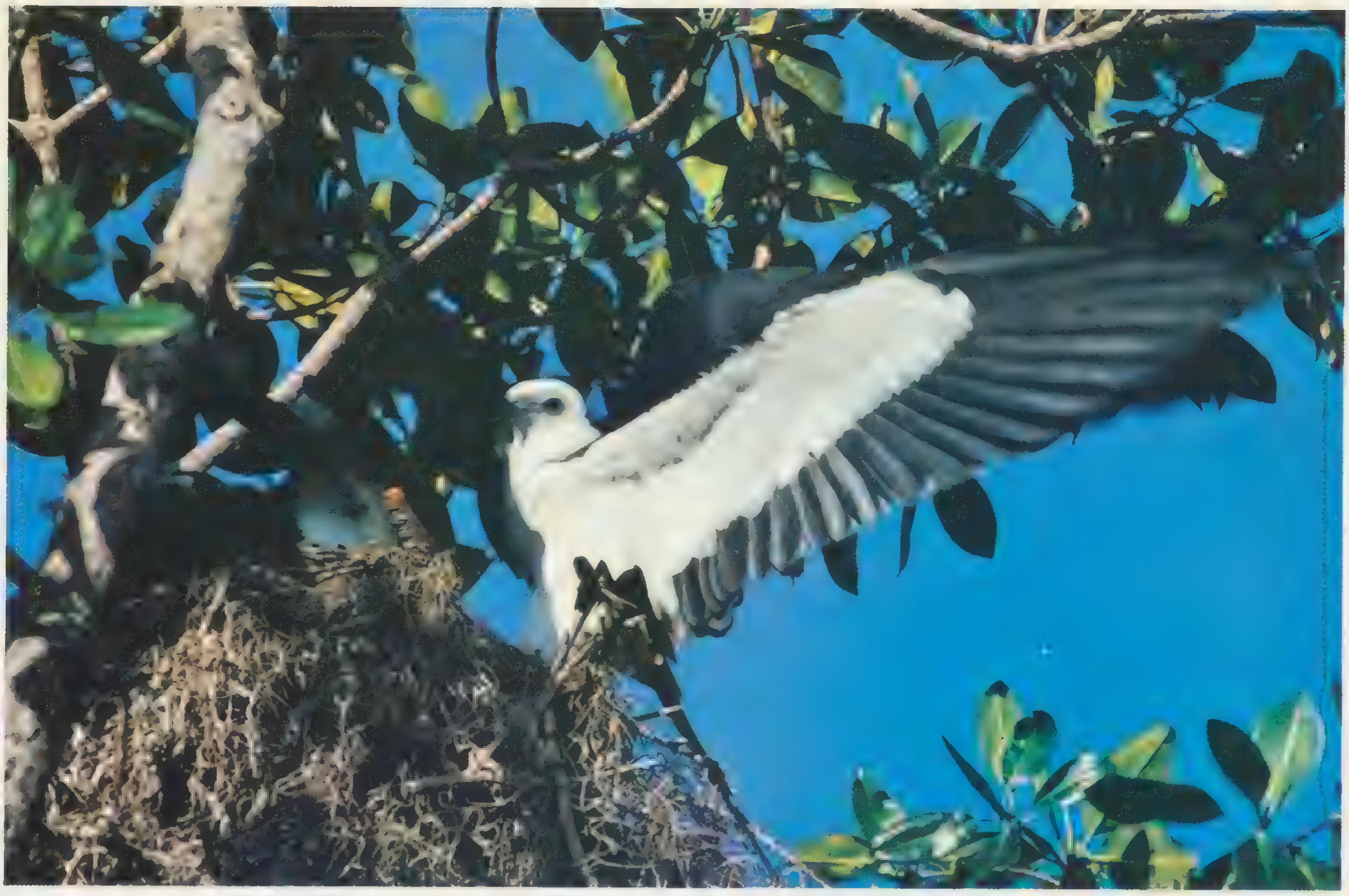
In 1970, a nest was built in the same tree crotch that held one of the 1969 nests, which had blown down. And in 1971, a pair of kites built about halfway between the two nests of 1969. Generally, about half a dozen kites frequented the study area. Apparently not all were breeding birds.

Sexing the birds was difficult, since no plumage dimorphism exists between males and females. However, one member of the pair studied in 1972 was distinctive because of a broken left outer rectrix. Its role in copulations clearly identified it as a male, and we were able to study division of labor between sexes of this pair with confidence. In 1969, once blinds were constructed, the four birds under study could be identified by slight differences in facial feather patterns visible at close range. Sex for these birds has been assigned by comparison of their nesting behavior patterns with the nesting behavior patterns of the birds of known sex in 1972.

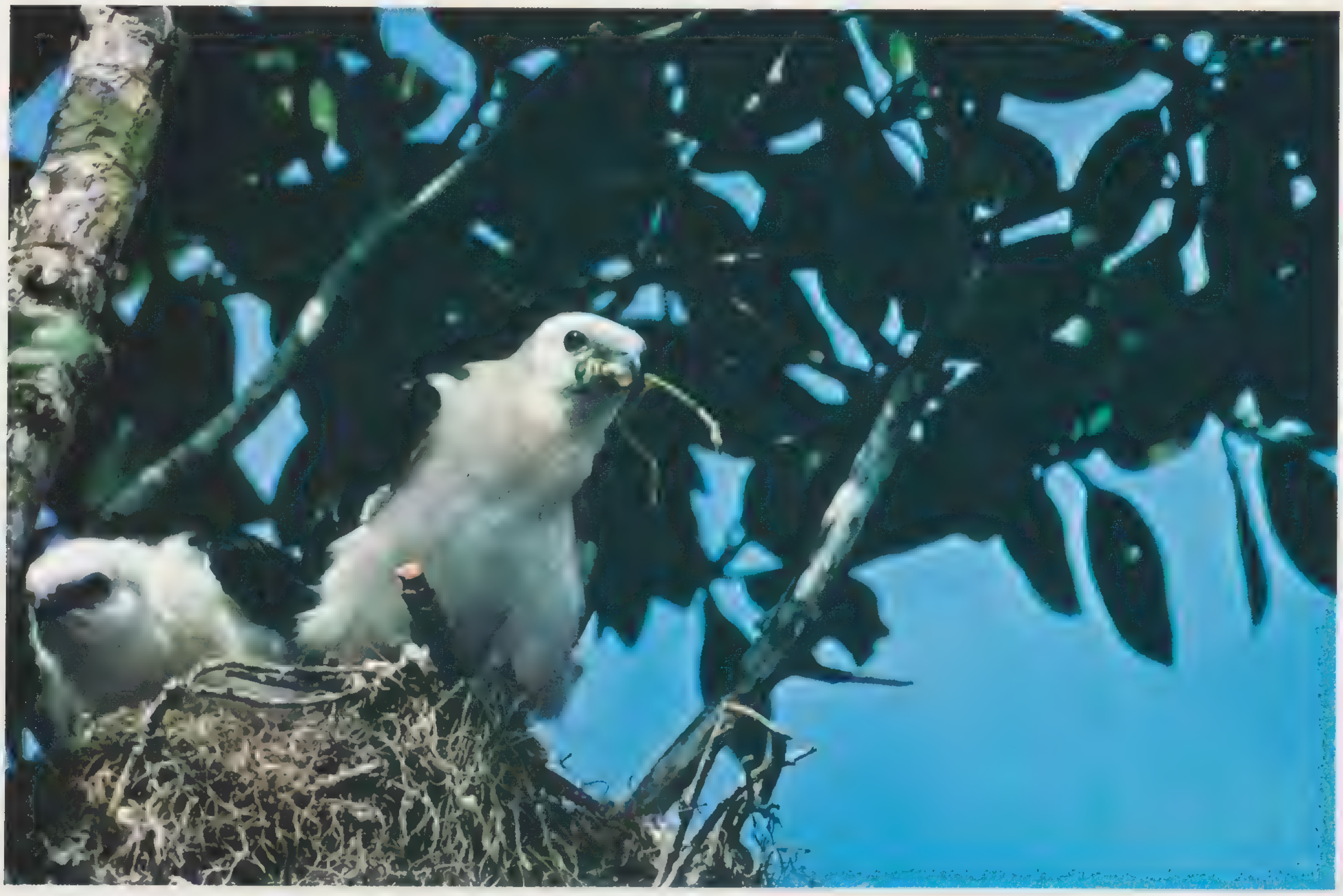
Arrival on the Breeding Grounds

Kites are generally first seen in southern Florida during the last week of February, but our earliest record for the species in the study area was 4 March, 1972. Migrating kites passing through the region often moved in loose flocks with pairing of birds evident. Whether these were actually male-female pairs and whether pairs keep together on the wintering grounds in South America is not known. In any event, the evidence suggests that at least some kites may arrive on their nesting grounds already paired.

During the early stages of residence in Florida, the kites spent much time soaring over their nesting areas (Figure 3). In the pair studied in 1972, the female characteristically cruised at a higher altitude than the male, although we do not understand the significance of this. The kites often engaged in conspicuous aerial interactions with one another, in which one kite, soaring at a higher altitude, swooped down to within a meter or so of



Swallow-tailed Kite (*Elanoides forficatus*) photographed in Everglades National Park by Frederick Kent Truslow. *Above,* parent with outstretched wings lands to feed young. *Below,* two young, one with a frog in its mouth.



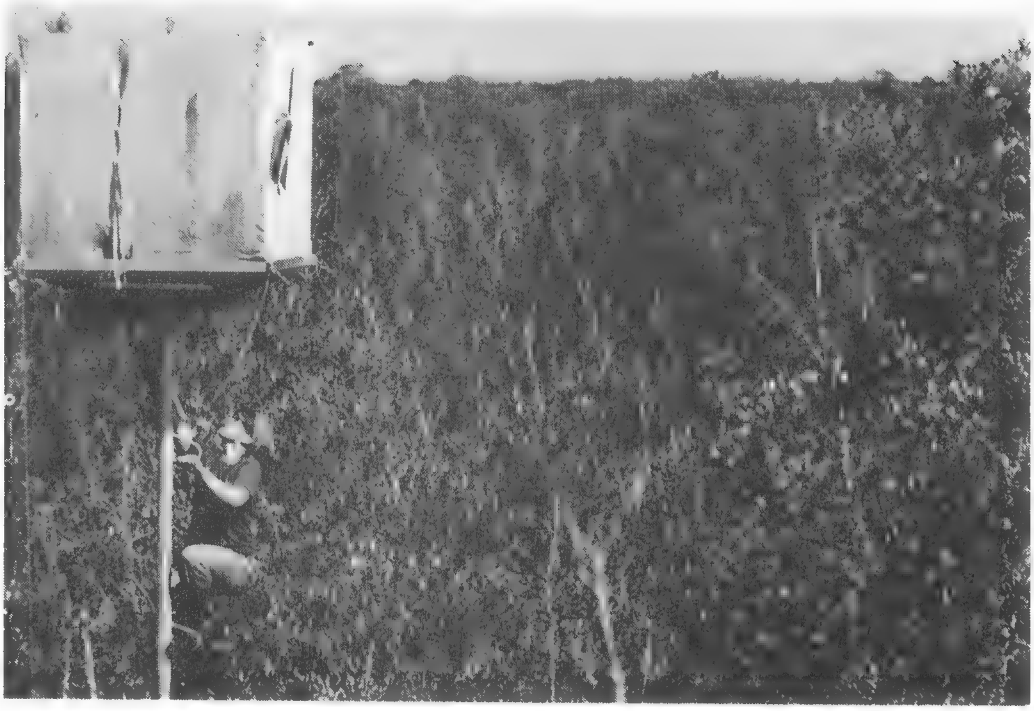


Figure 2. The active nest of 1972 (*top right corner*), like other nests studied, was located near the top of a black mangrove that was easily approachable from the air. Here, Helen Snyder enters the blind to observe the nest.

another kite. Such behavior occurred with both birds heading in the same direction (Figure 4). *Klee-klee-klee* vocalizations and sometimes *kees-a-we* calls generally accompanied the swoops. The lack of sexual dimorphism in the kites and the usual presence of more than two individuals in the study area ordinarily prevented us from determining whether or not such interactions took place between members of pairs. The male kite with the broken tail (1972) was sometimes on the receiving end of swoops and sometimes dove on other kites. On two occasions, it was clearly his mate that swooped down upon him, and on other occasions the male swooped down on birds other than his mate. The flight swoop displays may function in courtship and/or aggressive contexts.

The Nest-building Period

Soon after arrival, the kites commenced nest-building. In 1972, nest-building was in progress by 11 March, less than a week after arrival of the female of the pair.

During the nest-building period, the kites began their daily activities with preening and stretching on their roosting perches, usually dead black mangroves (Figure 5). The kites exhibited maintenance behavior with movements typical for raptors: direct scratching of the head with one foot, double wing-stretches over the back, and unilateral stretches with tail fanned out to one side (Figure 6).

Copulation

Copulations generally commenced early in the day, often before sunrise, and continued with apparently decreasing frequency as the day progressed. For example, in a full day of observation on 11 March 1972, we

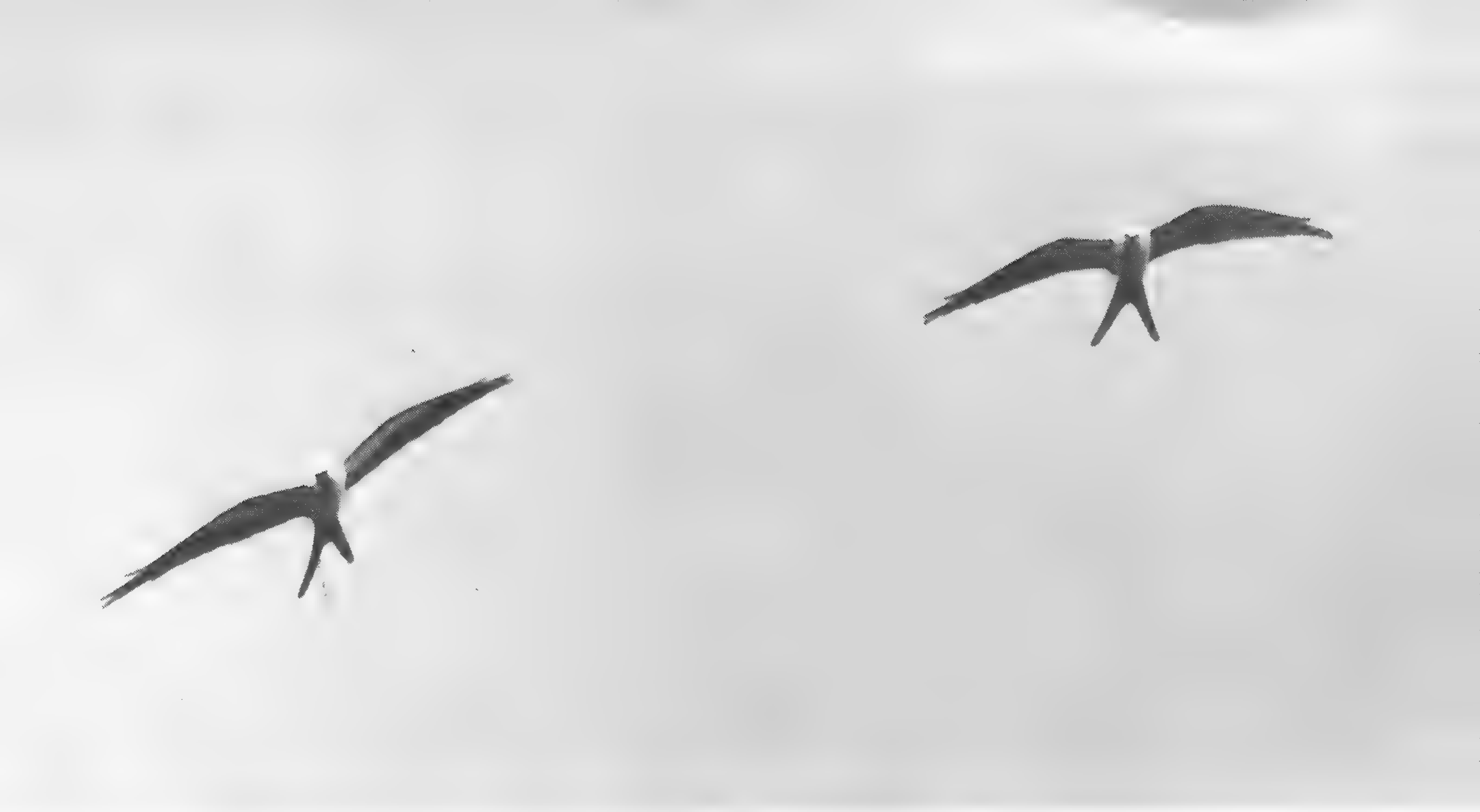


Figure 3. Kites soaring over the nesting area. In flight the birds maneuvered with subtle twisting of the tail and seldom flapped their wings.

recorded copulations at 06:38, 07:17, 07:36, 08:25, 08:56, and 12:40. One additional copulation apparently occurred at 15:00, but we saw it only imperfectly. However, since the birds were quite mobile and at times out of sight, we could not be certain that the above observations included all copulations which took place on the day in question.

Copulations, as observed in three different pairs, proceeded as follows: the female perched facing into the wind on an exposed horizontal tree limb. The male flew silently from another perch. As he neared the female, she bent forward with her neck outstretched and faced away from the approaching male with her wings slightly extended (Figure 7). The male landed directly upon her back. He then began to balance and adjust his position with wings drooped over those of the female (Figure 8). This silent period of adjustment usually lasted about 30 seconds. For the final three or four seconds on the back of the female, the male brought his tail under the female's, and his bill down onto her back (Figure 9). Almost immediately thereafer, he flew forward over her head, giving *klee-klee-klee* calls, while she remained perched uttering *kees-a-we* vocalizations. For one pair in 1972, the entire duration of mounting and copulation on eight occasions ranged from 28 to 37 seconds, with a mean of 31.6 seconds.

Copulations were confined largely to the nest-building period, but continued into the incubation period at one nest (1972). The last copulation of this pair that we saw was on 2 April, four days after the presumed laying of the last egg.

On one occasion I observed a copulation sequence that was followed immediately by a second one after the male had circled his mate twice at a distance of about 15 to 25 meters.

Nest-building

Generally, after an early morning period of preening, copulation, and foraging, which lasted an hour or two, the kites began gathering nest material. In the early stages of nest-building, they gathered largely dead twigs; but as the season progressed, they brought in proportionately more and more *Usnea* moss and occasionally Spanish moss (*Tillandsia usneoides*). The upper surfaces of the deeply-cupped nests were solid mats of moss.

The kites collected nesting material while in flight, in all instances observed. They circled low over the canopy, occasionally swooping to break off twigs or hunks of moss with their feet. They commonly dropped twigs after snapping them off, possibly because they were too small or were rotten. A kite often passed a twig back and forth between bill and feet, probably adjusting the material most effectively in the feet for transport to the nest (Figure 10). Although Skutch (1965) stated that the birds engage in such transfers to enable them to balance the material in the bill, I believe the opposite is the case, since we frequently observed birds carrying material in the feet for long distances — sometimes over a kilometer — without transferring it to the bill. However, on the final approach to the nest, a kite almost invariably transferred the material to the bill for landing. On only one occasion did I see a bird land with material in its feet, and this involved an exceptionally large branched twig.

Both sexes collect nesting material, but their relative contributions were difficult to determine during the pre-incubation stage because of the lack of sexual dimorphism. However, we could identify the sexes of one pair (1972) at this stage of the breeding cycle. Here, the male performed 7 of 13 nest-building trips observed, the female brought in material three times, and on three trips the sex of the bird carrying material remained unclear. At several nests one bird (the female at the 1972 nest) tended to remain for long periods arranging material, while the other devoted relatively more time to gathering twigs and moss. Gathering of nest material

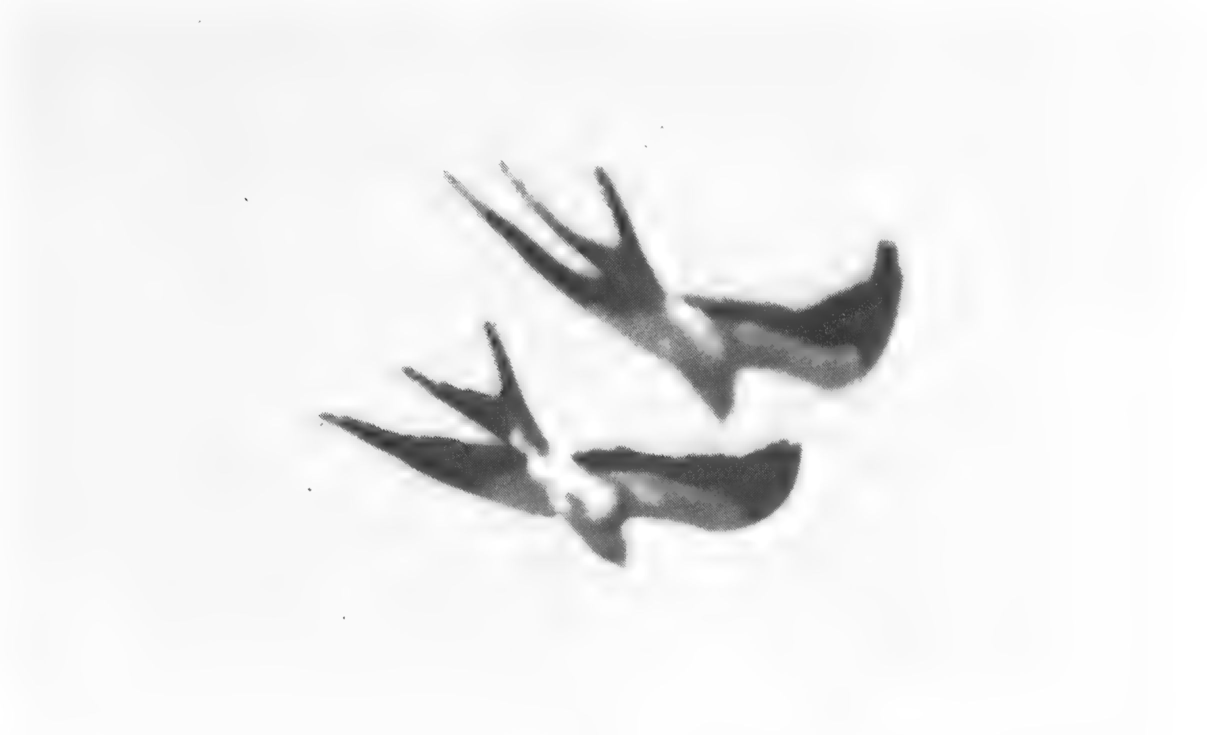


Figure 4. A diving-swoop interaction of a pair of kites. These swoops were generally accompanied by *kee-klee-klee* vocalizations and may function in courtship or in aggressive contexts.

during the incubation period was done primarily by males at all three nests studied closely.

Kites commonly gathered twigs within a few hundred meters of the nest site, but sometimes flew from great distances with nest material. The nearest known source of Spanish moss to the study area was approximately two kilometers away; yet the kites occasionally used Spanish moss in nest construction.

During the nest-building period, I sometimes observed the male feeding the female (1972). In all cases, the female perched on a dead limb facing upwind, while the male approached in flight from downwind, transferred the prey from foot to bill, landed momentarily beside the female, passed the food to the female, bill to bill, and then flew off calling *klee-klee-klee*. The female postured as the male approached, just as she did when the male flew in to copulate (Figure 7). In one instance the female appeared to initiate the transfer. She had been soaring high over the nest area when her mate returned low over the canopy with a lizard in his feet. The female abruptly swooped down to a nearby perch, and the male landed beside her with the food. On this same occasion, the transfer of food was immediately followed by a copulation after the male had flown one long half-circle around the female.

The proportion of the female's diet supplied by the male during the nest-building period was difficult to estimate. The female of one pair (1972), however, foraged on her own considerably at this stage.

Egg-laying and Incubation

The incubation period is approximately 28 days. This we determined as follows: at one nest (1969) incubation apparently started about 07:20 on

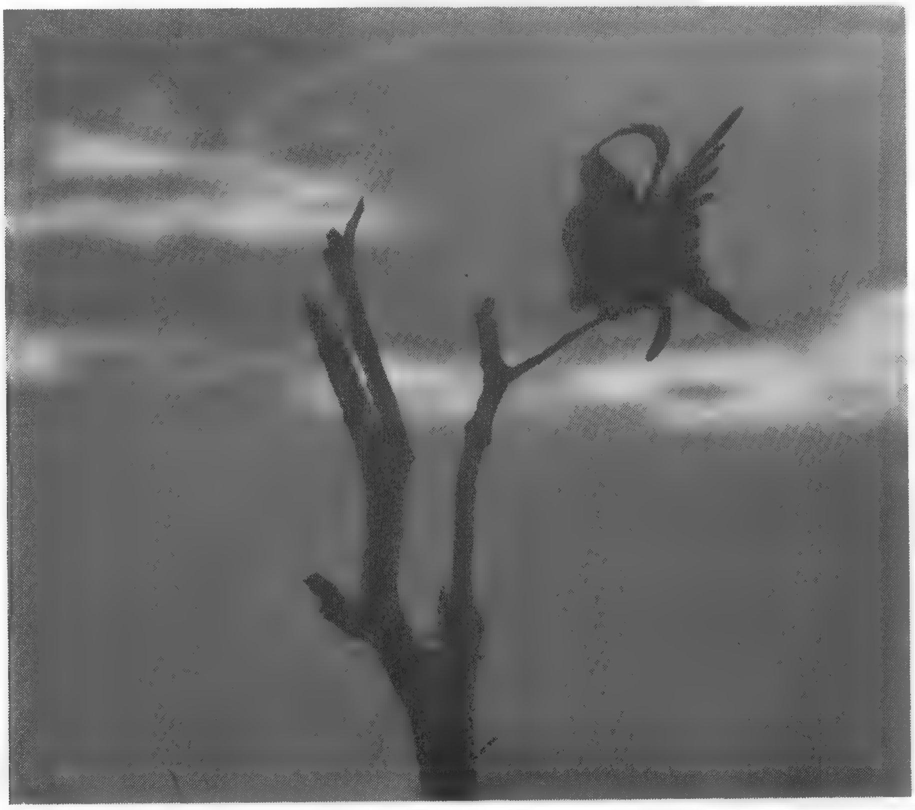


Figure 5. In the early morning, a Swallow-tailed Kite in a dead black mangrove preens its right outer rectrix.

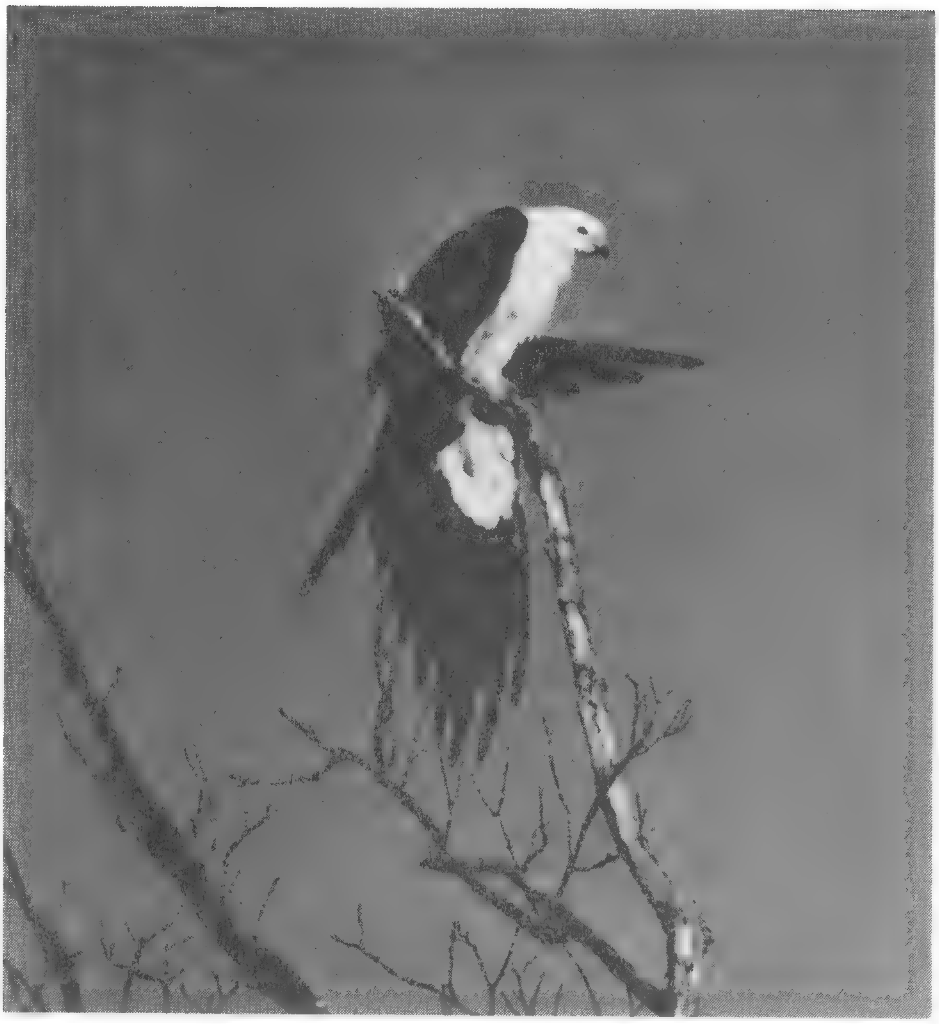
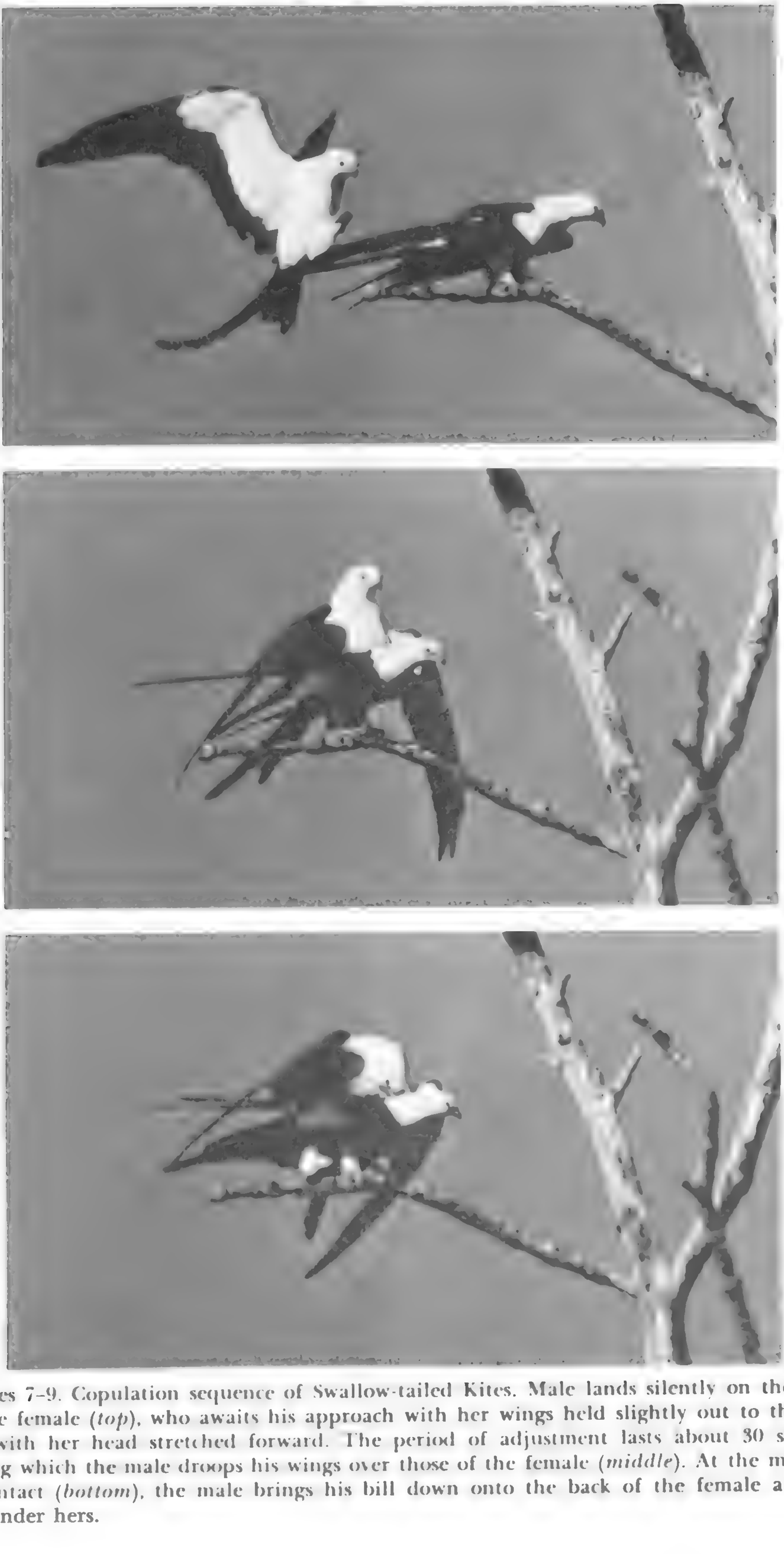


Figure 6. A unilateral stretch of a Swallow-tailed Kite on its roosting perch.

5 April, since the nest was unattended the previous evening and prior to 07:20. The nest was attended from 07:20 to 11:05, and at this time I left the study area. The single young of this nest hatched sometime between 15:00 on 1 May and 09:14 on 3 May. Thus, although I did not check the clutch size, 28 days was the maximum period of incubation. In 1972, the female of another nest sat close on the afternoon of 28 March. We climbed to the nest at 15:00 on 29 March and found two warm eggs. One egg in this nest hatched on the morning of 24 April and the second egg around noon on 26 April. Thus, the second egg was incubated for a minimum of slightly less than 28 days. If there is not a great deal of variability in the duration of incubation in the species, our data from the two nests demonstrate an incubation period of approximately 28 days. The interval between hatching of eggs at two nests (1969 and 1972) was about two days. Since the interval between laying of successive eggs possibly was also two days, incubation may have begun with the laying of the first egg.

When incubating, the kites generally faced into the wind, but occasionally faced in other directions with a light wind. The general consistency of position with respect to the wind contrasts with the frequent shifts in orientation seen in many other raptorial birds incubating eggs, and probably reflects, in part, the degree of exposure of kite nests to the wind and the precariousness of their nests at the tops of flexible mangrove trunks. One nest (1972), at the very top of a mangrove, was especially exposed to the



Figures 7–9. Copulation sequence of Swallow-tailed Kites. Male lands silently on the back of the female (*top*), who awaits his approach with her wings held slightly out to the side and with her head stretched forward. The period of adjustment lasts about 30 seconds during which the male droops his wings over those of the female (*middle*). At the moment of contact (*bottom*), the male brings his bill down onto the back of the female and his tail under hers.

weather (Figure 11). We found both young dead below the nest after severe storms. Apparently, strong winds had tossed them out of the nest.

Activities of the adults while incubating included occasional bouts of arranging nesting material, preening, probing into the nest bottom, egg-turning, and head-shaking if mosquitoes were dense. The study area in the mangrove swamp was exceptionally well-endowed with biting insects, including various sandflies, deer flies, and mosquitoes. Of these, only the mosquitoes appeared to bother the kites. Sometimes, when the wind was low in early morning, hordes of mosquitoes gathered around the treetop nests and caused the kites almost constant irritation. This problem was especially acute at two nests (1969, Figure 12), late in the nestling period. With even a moderate wind, mosquito swarms around nests quickly dispersed. Placement of nests near the tops of tall mangroves may be, in part, an adaptation to lessen exposure to mosquitoes, although it is probably more critically related to the difficulties these long-winged birds might have in maneuvering in denser vegetation at lower levels.

Incubation was performed predominately by the females; data from the three nests studied from blinds indicate that the females incubated overnight (8 observations). Males took one, two, or three shifts on the eggs during daylight hours, but their attentive periods averaged consistently shorter than those of the females for all three nests (Table 1).

Vocalizations from the bird on the nest characteristically, but not invariably, preceded nest exchanges. The incubating parent characteristically held its head low and stretched forward when calling. The calls employed by both sexes in this context were either *eeep* calls or *kees-a-we* calls, or a combination of the two — *eeep* calls leading into *kees-a-we* calls. Vocalizations accompanied 31 of 43 nest exchanges witnessed.

The relieving bird at a nest exchange often brought nesting material (Figures 13, 14, and 15). Of the 43 exchanges observed (20 males relieving females and 23 females relieving males), 25 incoming birds carried nest material (18 males and seven females). At two of the three nests, we saw no females bring nesting material during the incubation period. Nesting material brought in at this stage was invariably *Usnea* moss or twigs covered with *Usnea*.

TABLE 1

Duration of Attentive Periods during Incubation for Swallow-tailed kites[1]

	Male		*Female*	
Nest	*Mean attentive period (minutes)*	*Number of attentive periods observed*	*Mean attentive period (minutes)*	*Number of attentive periods observed*
1969, No. 1	49	6	128	4
No. 2	106	3	127	2
1972	118	13	178	5

[1] Only daylight hours and attentive periods bounded by undisturbed nest-exchanges are considered.

In only four of 29 nest-building trips seen during the incubation period, did the incoming bird fail to relieve its mate. All four cases involved males bringing in *Usnea* to females. In each case, the female's attentive period, had she left the eggs, would have been exceptionally short — considerably shorter than her shortest recorded attentive period. Probably, the decision to exchange duties at the nest depends upon how long the bird on the nest has been incubating.

Commonly, the bird relieved at the nest performed an aerial shake as it flew off. In this maneuver, the bird dove toward the ground with its wings pulled in toward the body, shaking its feathers. After a few meters of free fall, the bird extended its wings and soared onward. Sometimes, the relieved bird circled higher and higher over the nest, then sailed off into the wind in a long glide. This seems to be the preferred method for moving long distances upwind.

Although males fed their mates at the nest during incubation, females also foraged on their own at this stage, at least at the nest in 1972. The rates at which males fed females were much higher in 1969 than in 1972 (Table 2). I suspect this difference could be related to poorer food supplies in 1972. The lack of hylid frogs in the diet suggests some food stress for 1972; for these frogs comprised more than half the diet in 1969 (Table 3). Hylid frogs apparently had been largely eliminated from the mangroves by

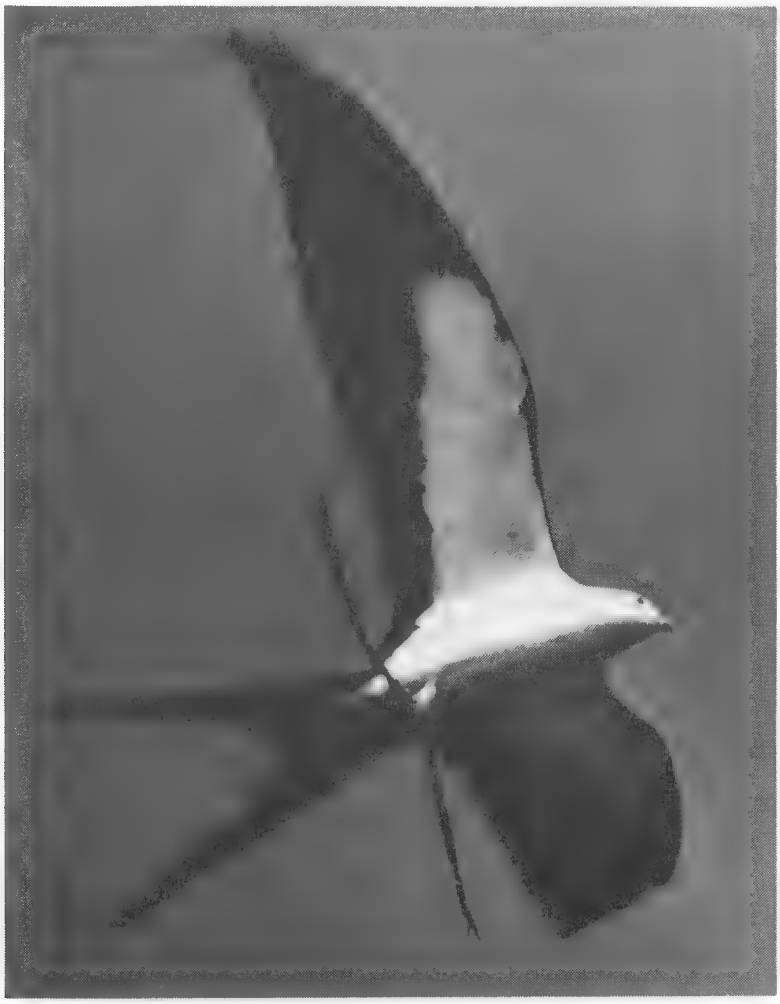


Figure 10. A Swallow-tailed Kite transports nesting material in its feet. During flights to the nest, kites frequently transfer nesting material back and forth from the feet to the bill in an apparent effort to get it properly balanced in the feet.

TABLE 2

Frequency With Which Males Fed Females at Nests During the Incubation Period

Nest	*Number of feedings observed*	*Hours of observation*	*Feedings per hour*
1969, No. 1	7	19.0	.37
No. 2	7	16.8	.42
1972	2	85.3	.02

the extreme summer drought of 1971. Although we commonly heard frogs in the study area in 1969, we observed none there in 1972. However, in 1972 hylid frogs were taken by kites from a fresh water region about 10 km inland.

The generally longer attentive periods of both sexes in 1972 compared with attentive periods at the nests of 1969 are also consistent with the hypothesis of food stress in 1972. Very likely the birds in 1972 needed more time to find sufficient food to satisfy their needs when off the nest (see Table 1).

As in nest exchanges, the female on the nest characteristically held her head low and stretched forward and gave *eeep* or *kees-a-we* vocalizations when her mate approached with food. Generally, the female trembled the wings slightly on her mate's approach. Food was passed from bill to bill, and the male usually flew off with *klee-klee-klee* calls immediately after the pass. On one occasion a nest exchange followed a food pass.

Hatching and Nestling Period

Hatching and the First Feeding

We witnessed hatching of both eggs at one nest (1972). In the process, the female spent considerable time chewing and apparently eating small

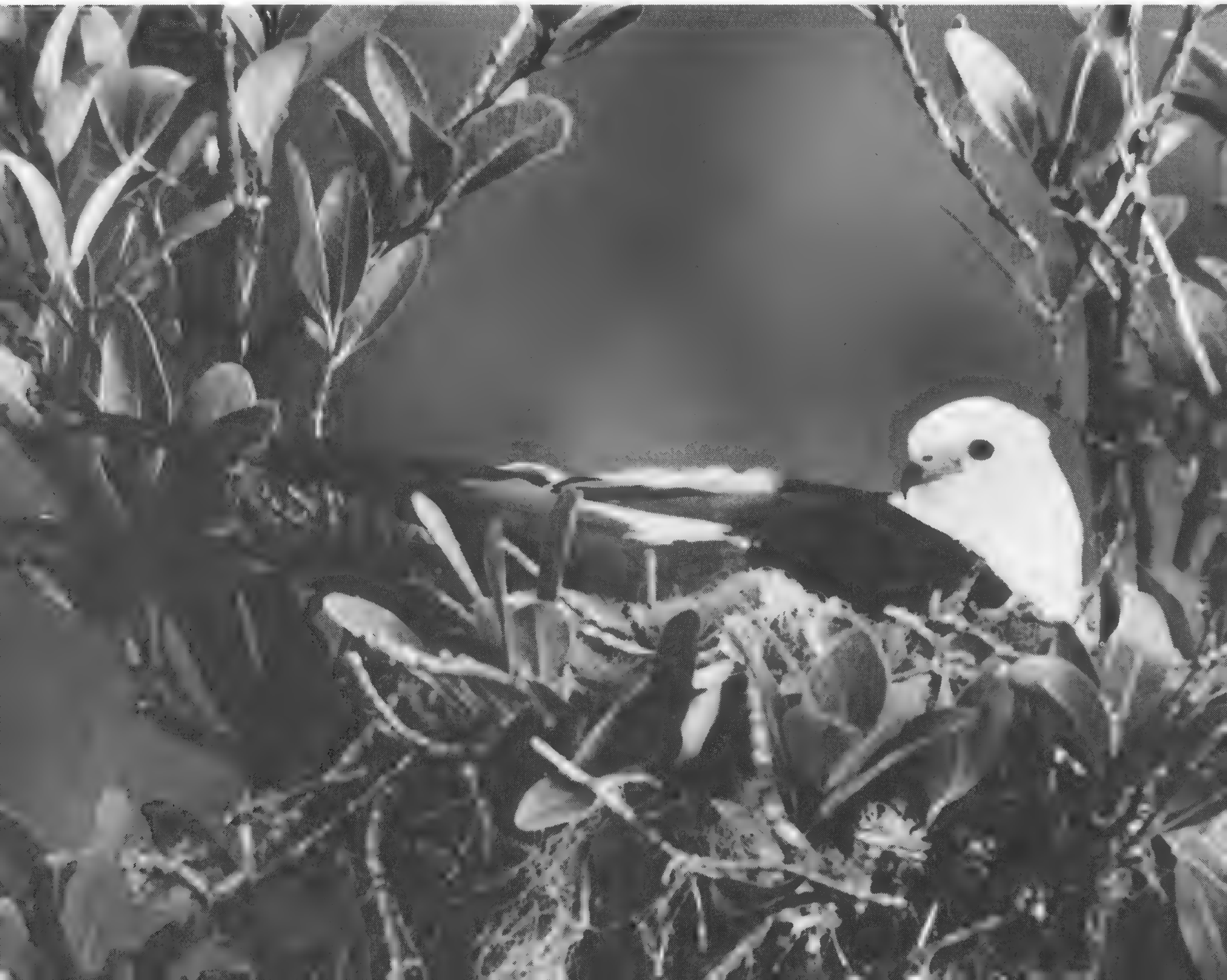
TABLE 3

Prey Observed at Nests of Swallow-tailed Kites

Nest or authority	*Insects*	*Frogs*	*Anole lizards*	*Snakes*	*Nestling birds*	*Mammals*	*Unidentified*	*Total*
1969, No. 1	1	19	6	—	1	—	3	30
No. 2	5	39	27	—	7	—	5	83
1972	—	—	5	1	9	—	1	16
Sutton (1955)	5	14	19	—	5	1	3	47
Wright *et al.* (1970)	30	20	—	1	8	—	40	99

shell fragments, including the allantois (a waste-filled sac, the outer wall of which forms an internal lining to the egg shell). On 24 April, hatching of the first egg had already begun by 09:30, judging from the restless behavior of the female. By 11:31, cheeping of the young was audible from the blind. At 11:44, the male relieved the female at the nest, and she took off on a remarkable flight of aggression around the near vicinity of the nest. At one point she pursued a distant Peregrine Falcon (*Falco peregrinus*), presumably a migrant, then returned to swoop repeatedly at the blind though I was motionless within. She had never before shown any aggression toward the blind. Finally, she returned to the nest at 13:06. At 13:21 the male brought in an anole lizard (*Anolis carolinus*), which she swallowed whole. Again, at 16:05, the male returned, this time with a nestling bird, and the first feeding of the chick commenced. The female placed the prey under her feet on the nest edge, and, with her wings held slightly out from her body, began ripping off small bits in her bill. These she held in front of the head of the chick (Figure 16). As in other raptor species, the chick actively grabbed at the food offered by the adult. During the first feeding, the chick ate only about two dozen bites of food; the rest of the prey was eaten by the female. Small bits that the chick dropped were carefully retrieved by the female and either offered again to the chick or eaten by the female. The first feeding lasted approximately 10 minutes.

Figure 11. A female Swallow-tailed Kite incubating eggs on the nest (1972). This nest, situated at the very top of a black mangrove, was especially exposed to the weather and failed when both young apparently were thrown out during thunderstorms.



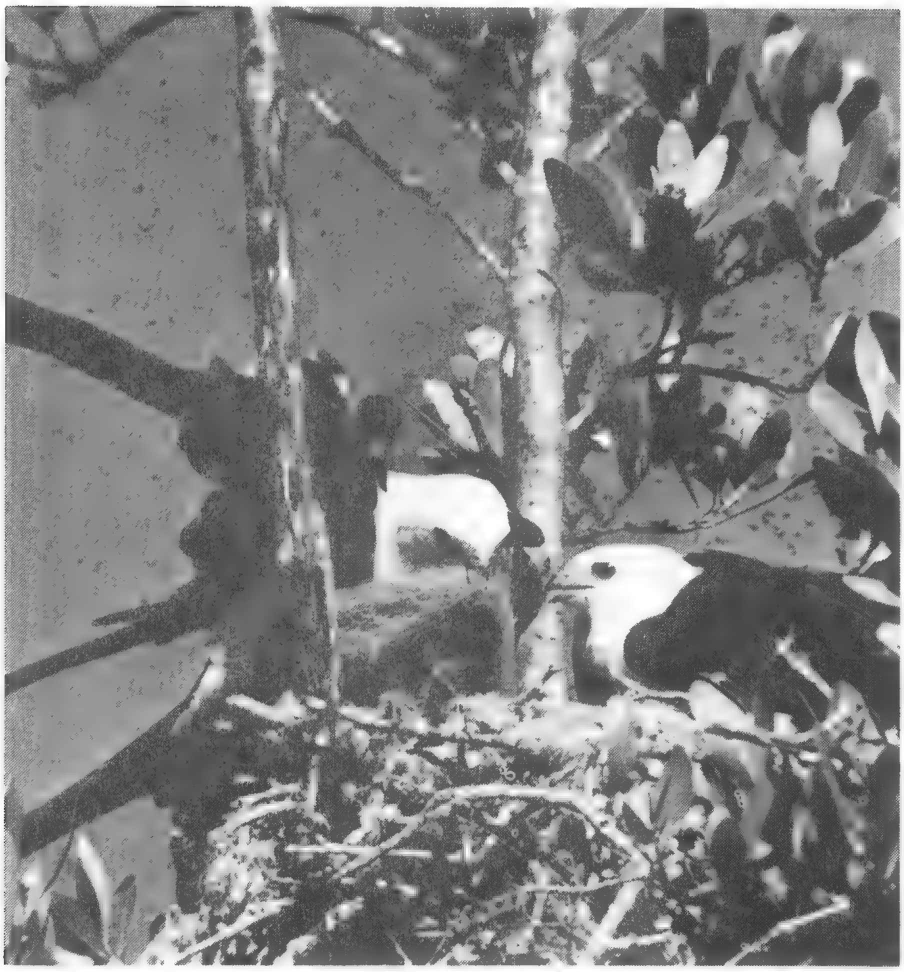


Figure 12. Nest-building late in the nestling period of one of the nests (1969). Swarms of mosquitoes — some 200 in this photograph — caused nearly constant irritation to the young (*right*).

Role of the Sexes during the Nestling Period

During the first part of the nestling period, females remained at their nests more or less continuously, brooding and feeding the young with prey brought to the nest by their mates. The males still occasionally relieved their mates at the nest and brooded the young during the first week; but thereafter, the role of the males was primarily in bringing prey to the nest (Figures 17, 18, and 19). The females dismembered prey for the young until the latter were about two to three weeks old and were able to swallow species such as anoles and hylid frogs whole. The female generally skinned hylid frogs when ripping them apart for the young, ate the skin and legs herself, and passed the rest to the young in pieces. Similarly, with anoles and nestling birds, structures such as the head, tail, and wings were generally eaten by the female after young failed in attempts to ingest them.

Toward the middle of the nestling stage, the females spent more time away from their nests, sometimes bringing in prey on their own. As the nestling stage neared termination, both sexes brought prey to the young and passed food to the bills of the young, who swallowed the items whole. Sutton (1955) described passes of food from the male to the female that took place away from the nest, followed by the female bringing the food to the chicks. We did not see such food passes in this study, but they may have occurred.

Occasionally, early in the nestling period, males arrived at their nests with prey when their mates were off the nest. Usually, the females soon returned, took the prey, and commenced feeding it to the young. On two occasions, however, the males eventually dropped the prey in the nest cup when their mates did not arrive, then settled down to brood both prey and young. I have never seen males rip apart prey for their young.

Feeding Rates

Feeding rates at the nest with two young (1969) averaged about twice the rates at the nest with one young (1969) — 2.2 versus 1.0 prey per hour, respectively (Table 4). At the 1972 nest, the second-hatched young was lost during a violent storm on the sixth day after hatching of the first young; the first-hatched young was lost in a second storm five days later. The relatively low rates of feeding at this nest again suggest a poorer food supply than in 1969.

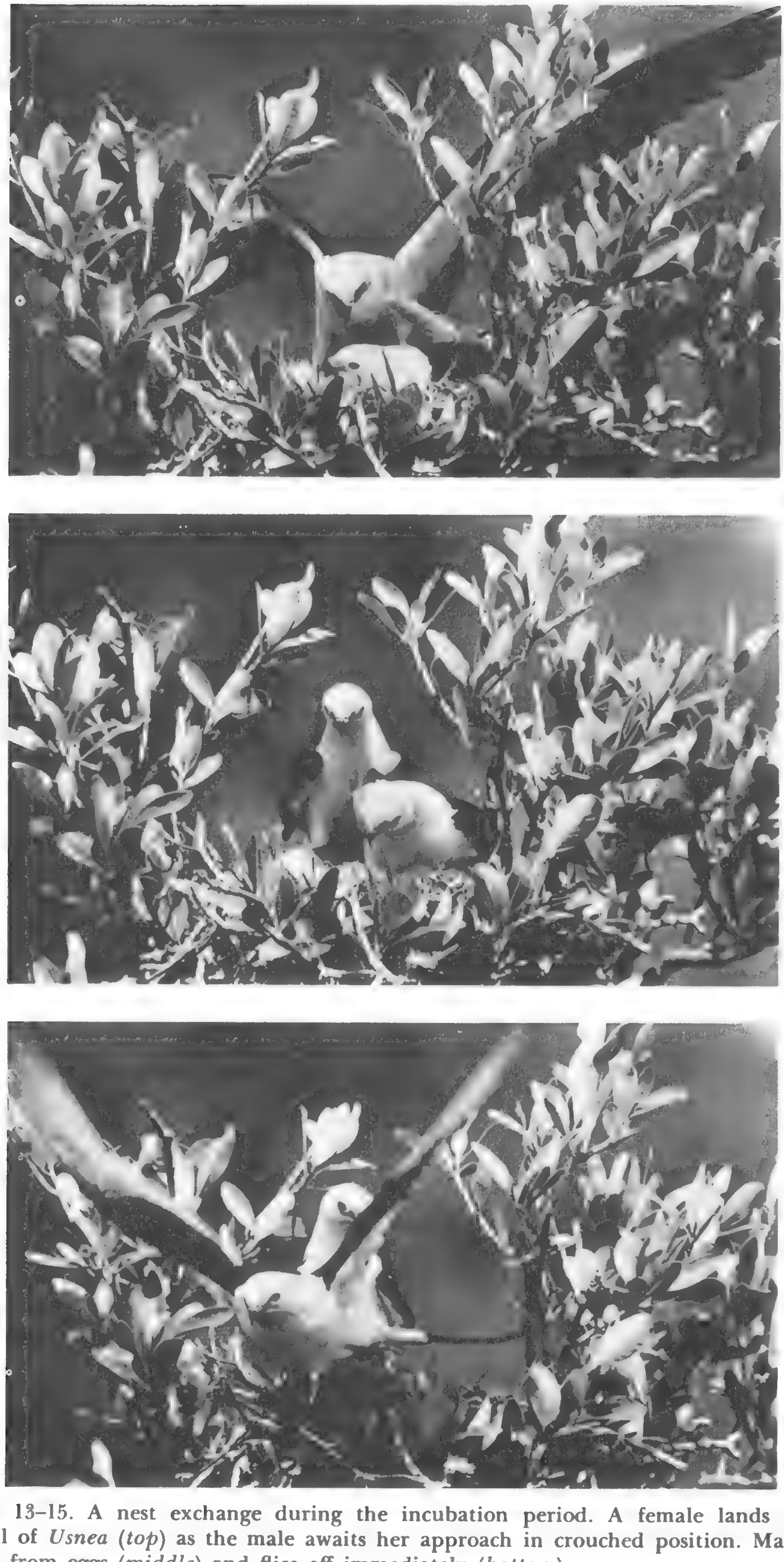
Nest Sanitation and Nest-building during Nestling Stage

During the early nestling period, nest-building nearly ceased at all three nests observed closely (Figure 20). During the fourth and fifth weeks of the nestling period, we witnessed renewed active nest-building at both nests in 1969 (Figure 12). This activity again usually involved *Usnea* and it appeared at a time when excrement from the young was becoming obvious on the edge of the nest. While there may be no causal connection between the buildup of excrement and the renewed nest-building, I think it is a strong possibility. *Usnea* moss forms a compact layer covering the excrement of the young and may function importantly in nest sanitation. The data of Sutton (1955) and Wright *et al.* (1970) also indicate renewed nest-building toward the end of the nesting cycle.

A remarkable feature of the behavior of nestling kites in the study area compared with the behavior of nestlings of other raptor species was an apparent inability to loft excrement over the nest edge. I repeatedly observed young backing up to the nest edge in typical raptor fashion, then, surprisingly, dribbling excrement directly down onto the nest edge. The extensive nest-building by adults late in the cycle served to cover the accumulation quite effectively, but one wonders why the birds have apparently lost the normal raptor behavior pattern of ejecting excrement beyond the limits of the nest. Possibly, it is an adaptation to reduce advertisement of the nest to terrestrial predators, especially raccoons, which abound in the mangrove habitat. The availability of an absorbent material such as *Usnea* moss may have facilitated the evolution of such a trait. In contrast, Wright *et al.* (1970) report normal raptor defecation over the edge of the nest they studied in open pine habitat in southern Florida.

Duration of Nestling Period

The length of the nestling period at one of the two nests in 1969 was between 36 and 39 days. At the other nest, it was 39 days for one chick and 41 days for the other. These figures compare closely with the 36-40 days at the nest studied by Sutton (1955), and an estimated 37-42 days for the nest studied by Wright *et al.* (1970).



Figures 13–15. A nest exchange during the incubation period. A female lands with a bill full of *Usnea* (*top*) as the male awaits her approach in crouched position. Male rises silently from eggs (*middle*) and flies off immediately (*bottom*).

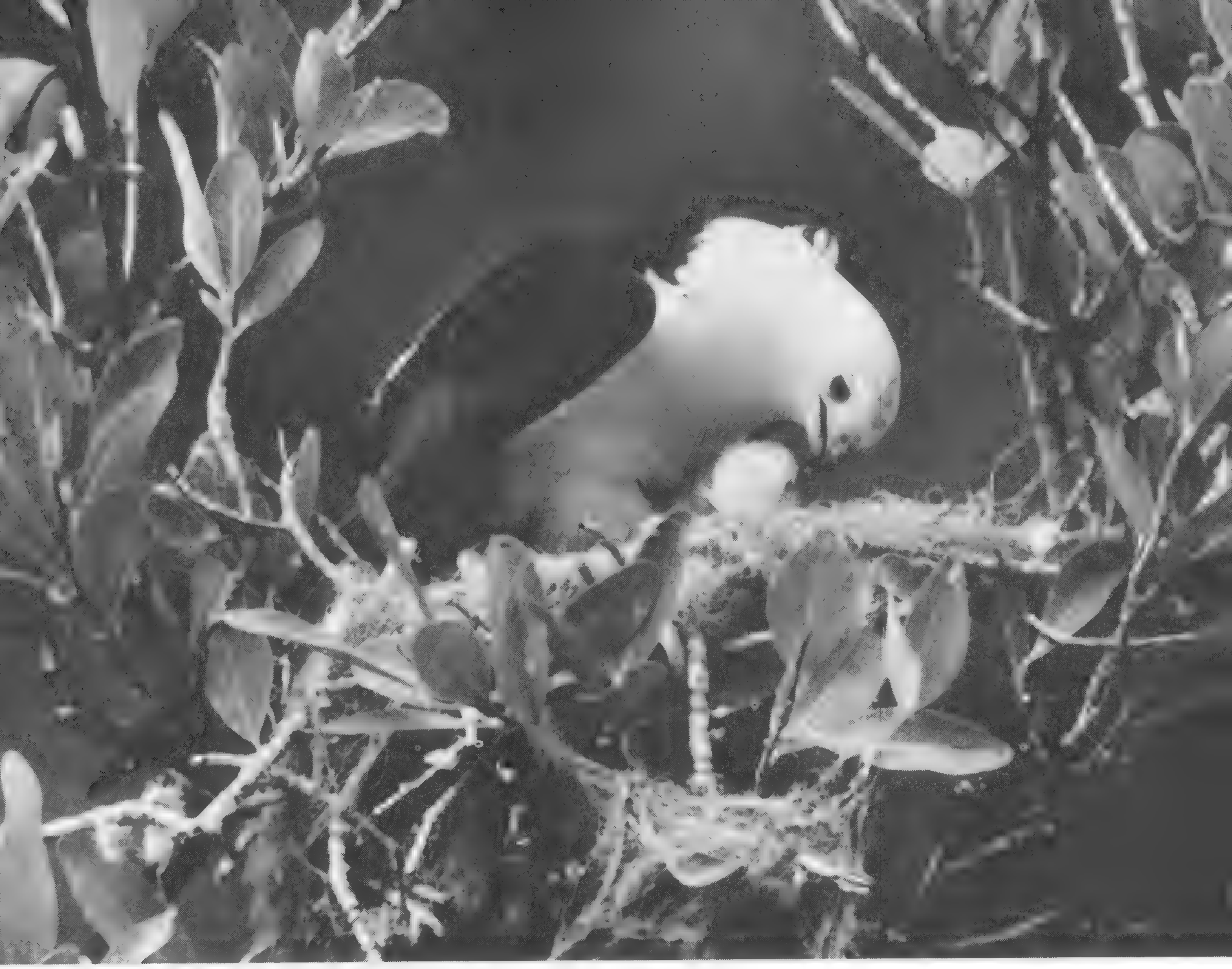


Figure 16. A female feeding a five-day-old chick. Bits of prey are held in front of the chick, which actively grabs them from the female's bill. Note the wings of the female held slightly out from the body and an anomalous brown stain on top of the female's head.

Development of Young

In 1969, we had no ladder to climb to the nests and gather detailed growth and development data. In 1972, such data were taken during the first two weeks, but the nest failed completely at this point. The fragmentary data of this nest are given in Table 5.

Feather development proceeds roughly as follows: nestlings are covered completely with white down for the first two weeks. At about two weeks of age, black primaries, secondaries, scapulars, and rectrices begin to emerge. At three weeks, buffy contour feathers appear on the head and breast; the scapulars appear solid black; and the wings are still a mixture of black and white in the folded position. By five weeks, the wings are solid black and the buff coloration of the head and breast is beginning to disappear, especially on the head. At the time of fledging, the buff has largely been replaced by white although traces are still present (see photograph in Wright *et al.*, 1971); the tail is distinctly forked but not so deeply as in the adults; and the general appearance is very much like that of the adults.

An interesting aspect of development noted in this study was the ability of the young to recognize their own species and whether or not their parents were carrying food. Newly hatched nestlings gave cheeping cries more or less continuously during the daylight hours, and especially during feedings. At about one week of age, cheeping cries of the young reliably followed the *eeep* calls of the female adult at the nest as the male approached with food. At this time the young also responded with cheeping cries when Great Crested Flycatchers (*Myiarchus crinitus*) gave *weep* calls in the vicinity of the nest. Sutton (1955) also noted young kites responding to the *weep* calls of Great Crested Flycatchers. The similarity of this call to the *eeep* call of the kites is apparent to humans as well. By two weeks of age, the young no longer responded to calls of the flycatchers. They did, however, call when adults came to the nest with or without food and when other large birds such as Common Grackles (*Quiscalus quiscula*) and Pileated Woodpeckers (*Dryocopus pileatus*) flew past the nest. By three weeks of age, the young no longer responded to large birds of other species flying past the nest, but still called when kites flew past with, or without, food. At five weeks of age, the young often failed to respond vocally when adults flew past the nest without food.

TABLE 4

Feeding Rates at Nests of Swallow-tailed Kites During the Nestling Period

Nest	*Number of young*	*Week of nestling period*	*Number of prey items*	*Hours of observation*	*Prey per hour*
1969, No. 1	1	1	3	2.75	1.09
	1	2	10	10.12	.99
	1	3	3	3.75	.80
	1	4	1	1.03	.97
	1	5	6	5.00	1.20
No. 2	2	1	18	11.61	1.55
	2	2	17	8.55	1.99
	2	3	17	5.38	3.16
	2	4	12	3.75	3.20
	2	5	6	3.00	2.00
	2	6	6	2.08	2.89
1972	2	1	8	16.00	.50
	1	2	5	10.67	.47
Sutton (1955)	2	1	8	13.17	.61
	2	2	9	8.17	1.10
	2	3	11	4.58	2.40
	2–1	4	16	9.00	1.78
	1	5	3	1.58	1.90
Wright *et al.* (1970)	1	3	14	23.92	.59
	1	4	21	27.15	.77
	1	5	12	14.97	.80
	1	6	50	12.50	4.00

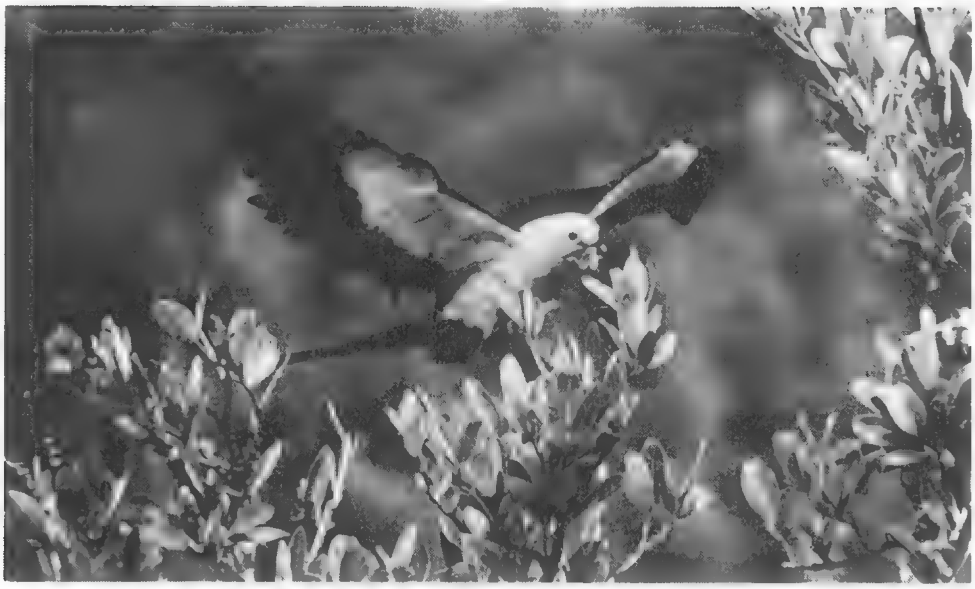


Figure 17. A sequence showing the passing of prey at the nest during the early nestling stage. The male transfers the prey — a nestling bird — from foot to bill in preparation for landing.

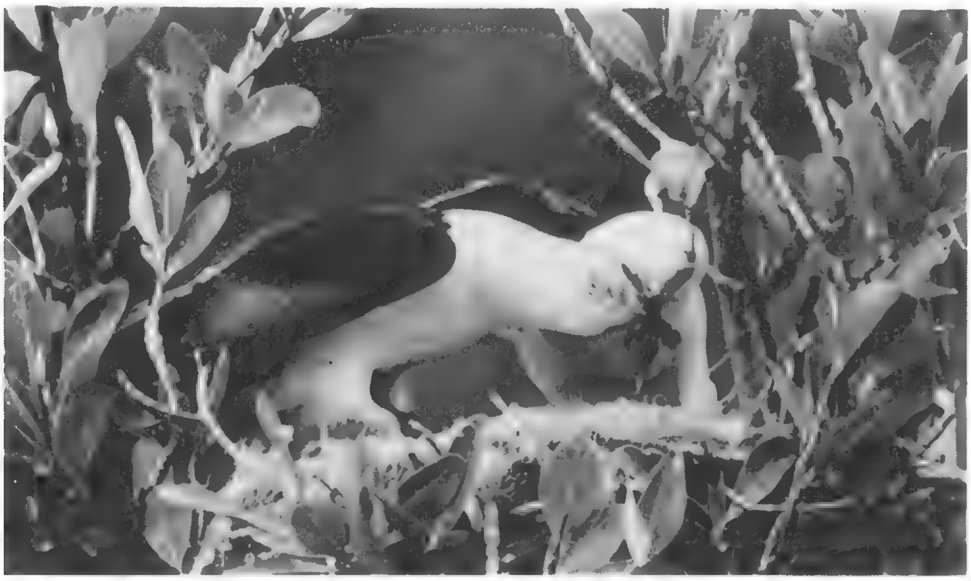


Figure 18. The female (*left*) grabs prey from the male's bill.

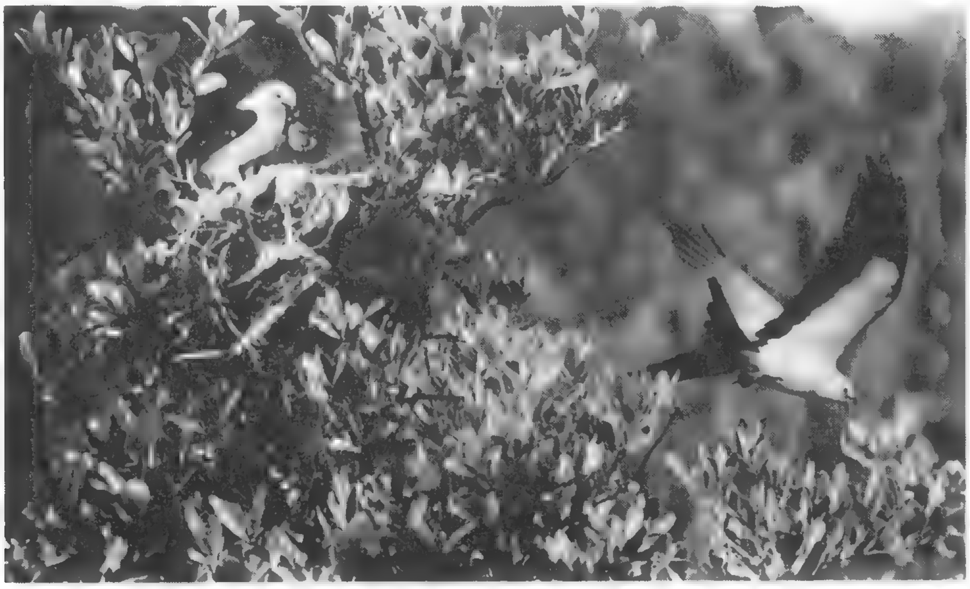


Figure 19. The male flies off immediately with ***klee-klee-klee*** vocalizations.

TABLE 5

Growth of Nestling Swallow-tailed Kites

Chick	*Day*	*Weight (gm)*	*Exposed culmen (cm)*	*Tarsus diameter (cm)*	*Wing chord (cm)*
No. 1	1	30	.79	.34	1.83
	3	34	.89	.34	2.00
	5	66	.95	.40	2.18
	8	100	1.08	.51	3.32
	12	220	1.34	.64	5.08
No. 2	1	26	.83	.42	1.90
	3	50	.88	.39	2.07
	4	—	.93	—	—

Post-fledging Period

Behavior of kites during the post-fledging period was not followed in this study, and the length of the dependency period after fledging is unknown. Wright *et al.* (1970) made observations of a young kite until two weeks after fledging. The youngster was still completely dependent on the adults at this time, and was being fed by both parents. Once the young kite had fledged from the nest, apparently it did not return. Adults defended the fledgling from approach by humans and Red-shouldered Hawks (*Buteo lineatus*).

Food

The kites I observed practised two different methods of aerial foraging — one for flying insects and the other for animal life resting on outer leaves and branches of trees. Kites caught flying insects in the feet after a brief swoop or a few flaps of the wings; they generally ate the insects on the wing. Sometimes the capture of an insect was so effortless that it did not even appear to disturb the soaring pattern of the bird. Generally it was impossible to identify insects caught high overhead, but dragonflies probably accounted for a large fraction of the species taken. In foraging for non-flying prey, the kites coursed low over, and among, the treetops, occasionally swooping down into the outer branches to grab a victim. Flight speed of foraging kites was timed roughly by automobile on several occasions and ran about 40 km per hour.

Diet for the three nesting pairs given in Table 3 include only items brought to nests. While this gives a reliable estimate of diet for nestlings, it may give a biased estimate of total diet for the kite families during the nesting period. Adults brought very few insects to the nests, although I often observed adults hawking insects and believe that such food may form a significant fraction of adult diet.

Green hylid frogs (*Hyla cinerea* and *H. squirella,* presumably) formed the bulk of the nestlings' diet in 1969. Both pairs also commonly brought anole lizards and lesser numbers of nestling birds and insects to the nests. Insects included dragonflies (2), tabanid flies (2), and, in one case, a paper wasp nest (counted as one insect prey though it contained a number of larvae).

Diet for the 1972 nest was strikingly different from that of the 1969 nests, as it included no hylid frogs. I identified one nestling bird in the diet as a woodpecker, almost surely a Red-bellied Woodpecker (*Centurus carolinus*).

The diet in 1969 compares closely with data given by Sutton (1955) for a kite nest in a mangrove area not far from the study area considered in this paper (Table 3). The data of Wright *et al.* (1970) for a pair nesting in open pine woodland are characterized by a large number of unidentified prey (Table 3). Whether these unidentified prey lead to a strong bias in interpretation of proportions of various prey types in the diet of the pair studied is unclear. In any event, this pair brought many more insects to the nest than the pairs either Sutton (1955) or I observed.

In the pairs observed in this study, unidentified food items were those not visible because the adults had their backs to the blind or because the attention of the observer was drawn to some other occurrence at the time of feeding. We identified all prey observed.

Vocalizations

The vocalizations of adult Swallow-tailed Kites are rather uniform spectrographically (Figure 21). Aurally, there appear to be three kinds of

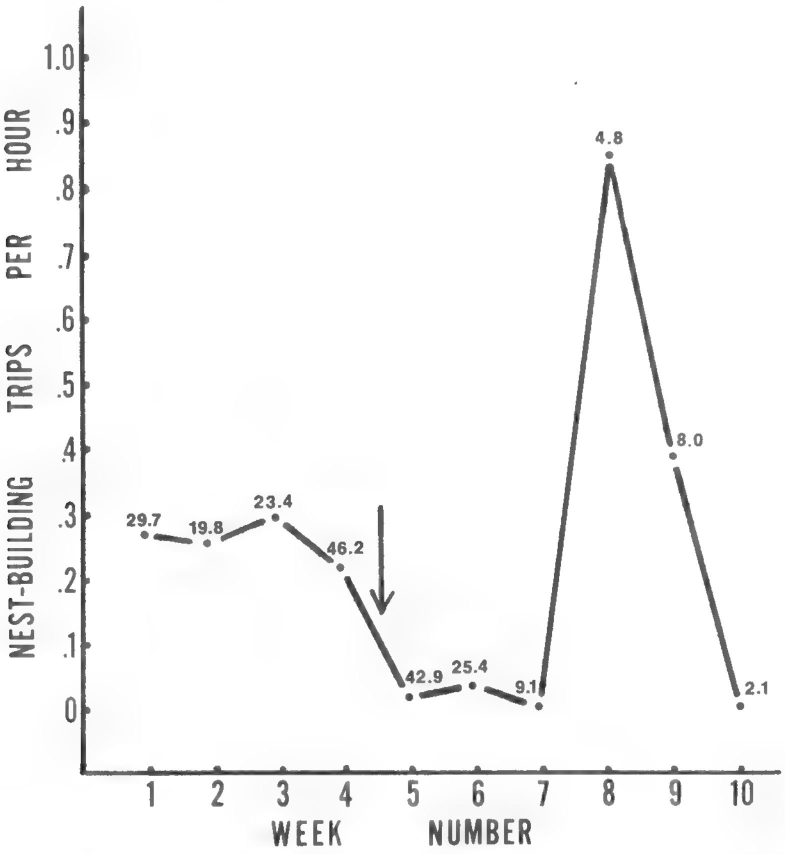


Figure 20. Rates of nest-building of Swallow-tailed Kites during the incubation and nestling stages (data of three nests combined). Arrow indicates the hatching of eggs. Numbers over each point indicate hours of observation during the week in question.

adult calls, but all three are built on the same basic unit, which is a short note rising about a kilohertz in frequency, then falling again. The three calls — *klee-klee-klee, eeep,* and *kees-a-we* — are given by both sexes. The frequency of the males' calls averaged about .5 kilohertz lower than the frequency of the females' calls in the pairs recorded.

Kites give the *klee-klee-klee* call in situations of strong excitement or alarm. The *klee* syllable is characteristically heard in groups of three, although sometimes fewer or more *klees* are given. Contexts in which we have heard this call include: (1) interactions with potential predators, (2) display swoops early in the nesting season, (3) following copulation or food transfer by males, and (4) soaring overhead in groups.

Adults render the *eeep* call primarily either when passing food from one bird to another or when exchanging places at the nest. Spectrographically, the *eeep* call is similar to a single *klee,* but is more drawn out and sounds less sharp to the ear. *Eeep* calls are often repeated a number of times, but there does not appear to be any characteristic number of repetitions. Not uncommonly, this call leads into the *kees-a-we* vocalization, which appears to be a higher intensity call used in similar contexts.

The *kees-a-we* call appears to be built out of two basic rising-falling notes in which the emphasis changes from one note to the next. Aurally, one hears a three-syllable call which is strongest on the first and third syllables. The first syllable emphasizes the high frequency middle portion of a basic note; the middle syllable represents the initial rising phase of the next basic note; and the last syllable represents the high frequency middle portion of the same note as the middle syllable. The number of *kees-a-we* calls given in succession varies but usually runs between two and four. We have heard the call from (1) males and females on the nest at approach of their mates, (2) females after copulation, and (3) occasionally during diving-swoop interactions.

In addition to the above adult vocalizations, young chicks also give distinct cheeping cries (Figure 21), which resemble the basic adult note with their rising and falling frequencies. Calls of small young are much higher in pitch than calls of the adults. By the time they are close to fledging, however, nestlings give *eeep* and *kees-a-we* calls that are very similar to calls given by an adult when its partner approaches the nest with food.

Social Relationships

Swallow-tailed Kites are conspicuously gregarious in migration, feeding, and nesting. I have recorded no defense of feeding territories, although I saw intraspecific chases, possibly territorial, in the immediate vicinity of nests. Nevertheless, on numerous occasions I watched kites from elsewhere forage unopposed within a hundred meters of an active nest and observed members of nesting pairs join other kites nearby in foraging groups. At times during the nesting season, I saw as many as 18 kites foraging together for dragonflies over a swamp.

Skutch (1965) discusses the presence of additional adults in the vicinity of nesting pairs without clarifying its significance. In 1969, we usually observed six kites in the study area — two active nesting pairs and two additional birds that commonly roosted between the two active nests approximately 200 meters apart. In 1972, a single extra kite associated closely with the nesting pair early in the nesting season, but this bird later drifted off. I

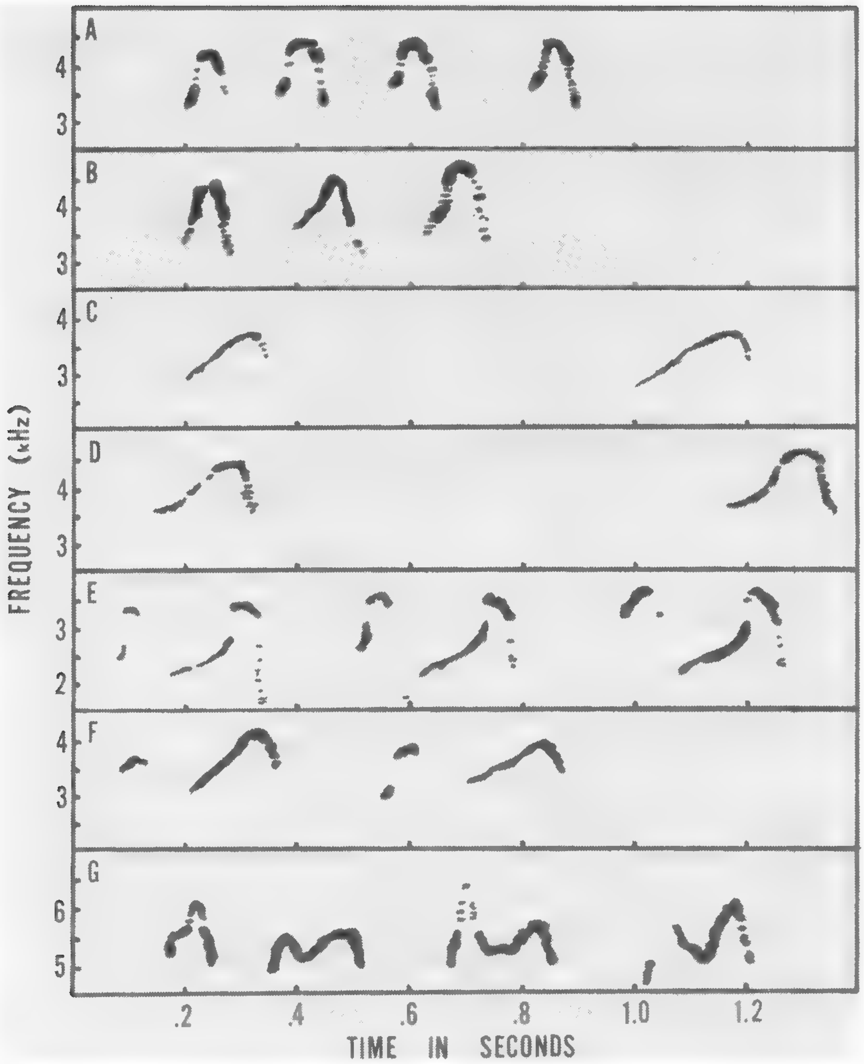


Figure 21. Sonograms of vocalizations of Swallow-tailed Kites: A, *klee-klee-klee-klee* call of male; B, *klee-klee-klee* call of female; C, *eeep* calls of male; D, *eeep* calls of female; E, *kees-a-we* calls of male; F, *kees-a-we* calls of female; G, cheeping of a seven-day-old chick.

have no evidence that extra adults ever participated directly in nesting activities.

Since the 1972 data suggest that kites may sometimes suffer some stress from low food supplies in the nesting season, one wonders what advantages may accrue from semi-social assemblages at this time. I believe the answer may lie in relationships with predators. I have repeatedly observed instances in which kites collaborated in harassing potential predators such as Bald Eagles (*Haliaeetus leucocephalus*) and Great Horned Owls (*Bubo virginianus*). Groups of kites may be more effective in discovering and deterring these predators than single birds or pairs. If so, breeding pairs may benefit from nesting close together and from the presence of extra birds.

Interactions with Other Species

Swallow-tailed Kites have been seen harassing a variety of potential predators including the Common Crow (*Corvus brachyrhynchos*), Bald Eagle, Red-shouldered Hawk, Great Horned Owl, Barred Owl (*Strix varia*), Peregrine Falcon, raccoon (*Procyon lotor*), and humans. The response consists of aggressive swoops accompanied by loud *klee-klee-klee* calls, which apparently serve to draw in other kites from the vicinity. In 1972, when I climbed the nest to measure young, aggressive behavior by the parents generally resulted in a gathering of some six or seven adult kites calling overhead. Only the female of the pair actually dove at me. With other predators, I saw harassing dives by many members of a group of kites.

Kites also commonly responded with alarm when Ospreys (*Pandion haliaetus*) and Turkey Vultures (*Cathartes aura*) came into the nesting area. Nevertheless, kites did not give alarm responses to all large or soaring birds. I did not see the kites chase Brown Pelicans (*Pelecanus occidentalis*), Roseate Spoonbills (*Ajaia ajaja*), or various herons that passed through the area. Ospreys and Turkey Vultures possibly represent something of a threat to young in the nest. Recent observations indicate that Ospreys are not completely restricted to a fish diet (Tait *et al.*, 1972; Wiley and Lohrer, 1973) and Turkey Vultures have been known to practice predation (Brown and Amadon, 1968). Probably the most significant enemies of the kites are Bald Eagles, raccoons, and Great Horned Owls. As discussed earlier, since nestling kites avoid defecating over the nest edge, this may be an adaptation to avoid advertising the nest to raccoons. Another feature of kite behavior, which appears to function in discouraging discovery of the nest, is the absence of alarm vocalizations when kites are surprised by a terrestrial predator in the vicinity of the nest. When I approached the 1972 nest to check eggs or young, the bird on the nest invariably left silently, then started calling in alarm at some distance, coming overhead to circle and call continuously until I had moved off to a distance of a hundred meters or so from the nest. This behavior, coupled with the inconspicuousness of the nests viewed from the ground, makes it very difficult to find kite nests even when the approximate position of nests is known from movements of the birds.

Kites generally place their nests in sites that are visible from above. From the air, the white heads of attending adults render the nests conspicuous. When incubating, however, the birds remain almost constantly alert to their surroundings, leaving the nest quickly when an eagle appears in the distance. With the adults away, the nest with its spotted, inconspicuous eggs is much more cryptic. The nestlings, however, are white. As the nests are often directly exposed to the sun, white coloration may be important in reducing heat stress for the young, and this factor may outweight the disadvantage of conspicuousness to aerial predators. Alternatively, white coloration of nestlings may be adaptive in rendering them maximally conspicuous to adults, thus reducing the chances of adults accidentally pinning the young with their talons as they land on the nest.

One active kite nest found in a mangrove area just outside the study area in 1972 failed because of predation on one of the adults. I found dismembered remains of this bird directly under the nest. I suspect the predator may have been a Bald Eagle, a species common in the area.

Summary

During 1969 and 1972, a total of three pairs of Swallow-tailed Kites were observed closely from blinds during the breeding season in southwestern Florida. Additionally, less detailed notes were made on other nesting pairs of kites in the region.

Kites generally arrived in southwestern Florida during the last week of February or first week of March. Nesting activities began immediately. During early stages, kites spent considerable time soaring over their nesting areas, often engaging in conspicuous aerial swoops on one another. Copula-

tions were most frequently observed in early morning and took place on exposed perches, lasted approximately 30 seconds, and were followed immediately by vocalizations. At the 1972 nest, copulations continued into the incubation period.

Kites built their nests at the tops of relatively tall and isolated black mangroves. Nest-building involved both sexes, with males gathering more material than females. It continued at a regular rate through the incubation period, when it was generally associated with nest exchanges. During the early nestling period, nest-building nearly ceased, but became frequent again in the late nestling period. Dead twigs were the predominant nest material in the early stages. Later, the material collected was almost invariably moss (*Usnea* moss or Spanish moss), or twigs covered with moss. Nesting material was collected with the feet while in flight and was generally carried in the feet with occasional brief transfers to the bill. When landing, it was almost invariably transferred to the bill.

Females performed the bulk of incubation, including all overnight shifts observed. Males incubated one to three shifts during the daylight hours, but these attentive periods averaged considerably shorter than female shifts during the daylight hours. Males commonly fed females at the nests during 1969 when hylid frogs were abundant, but at the 1972 nest such feedings were rare. At the 1972 nest, the female foraged on her own during the incubation period, which lasted approximately 28 days. The young hatched asynchronously. Hatching of the eggs was witnessed at the 1972 nest. Eggshells were not removed from the nest but were chewed and partially eaten by the female. The young first received food approximately five hours after hatching of the first egg.

During the first part of the nestling period, females remained at their nests, brooding the young and ripping apart prey for them. Males performed nearly all the foraging at this stage. Males were never observed tearing up prey for the young. Males occasionally brooded young. By the mid-nestling stage, young were able to swallow most prey whole, and females spent increasing amounts of time away from their nests. Toward the end of the nestling period, both adults brought in prey to the young. Nestling kites avoided defecating over the nest edge. This may be an adaptation to reduce advertisement of the nest to terrestrial predators. The nestling period lasts approximately 40 days, with some variability.

Nestling kites showed steadily increasing discrimination in the use of their begging calls. When small, they called in response to many stimuli, including the calls of unrelated species. When near fledging, young generally limited their calling to times when adults approached with food. At fledging, young kites closely resembled adults in coloration with the exception of some buffy coloration left on the head and breast. Tails were still not as deeply forked as those of adults.

Food consisted of relatively small prey, primarily hylid frogs, anole lizards, insects, and nestling birds. All prey captures observed were in the air (insects) or on the outer branches of trees. Few insects were brought to nests, although insects were frequently taken by adults. Nestling diet in 1969 was primarily hylid frogs. Frogs apparently were eliminated from the study area by the extreme drought of 1971, and nestling diet in 1972 was primarily anoles and nestling birds.

Adult vocalizations consisted of three types: the *klee-klee-klee* call, the *eeep* call, and the *kees-a-we* call. All three are built on the same basic note which rises and falls approximately a kilohertz in frequency. Contexts are described for the use of each vocalization.

Swallow-tailed Kites tend to be gregarious in nesting, foraging, and migration. A primary advantage may lie in enhanced abilities to detect and deter potential predators. Numerous examples of cooperative assault on eagles and owls were observed during the study. Kites also responded with alarm to other potential predators, including Ospreys and Turkey Vultures.

Acknowledgments

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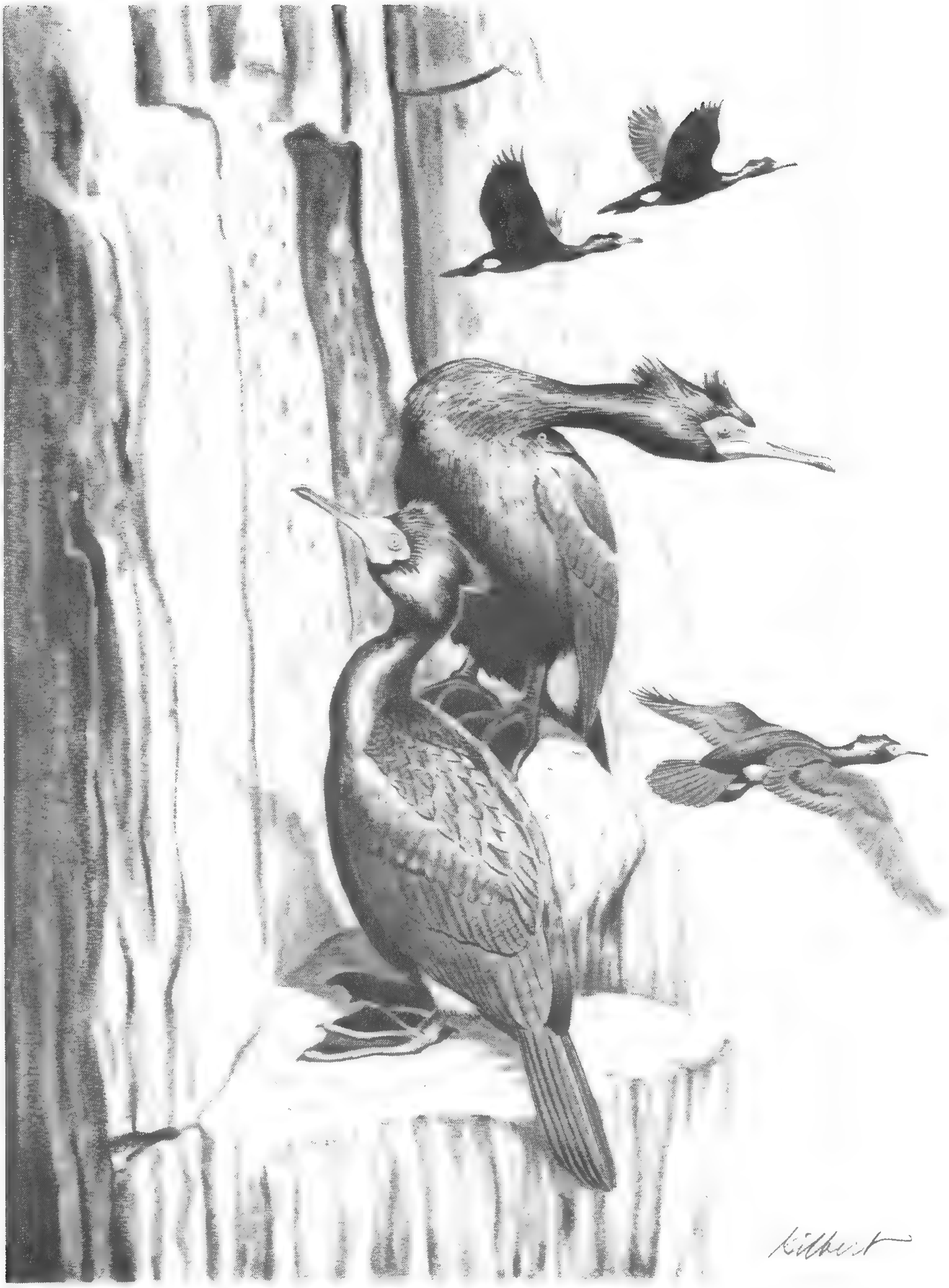

Red-faced Cormorant, *Phalacrocorax urile*. Drawing by Albert E. Gilbert.

THE RED-BILLED TOUCAN IN GUYANA

Godfrey R. Bourne

Photographs and illustrations by the author

Toucans constitute a family of birds popularly exhibited in zoos and pet stores. Their distribution extends from the forests of southern Mexico through tropical and subtropical South America. Although the family of toucans includes 41 species (Meyer de Schauensee, 1966), few detailed studies have been made on natural populations.

Van Tyne (1929) published a life history of the Keel-billed Toucan (*Ramphastos sulfuratus*) in Panama. Wagner (1944) studied the breeding behavior of the Emerald Toucanet (*Aulacorhynchus prasinus*) in Mexico. Skutch (1944, 1967b) published his observations of the Blue-throated Toucanet (*A. caeruleogularis*) in Costa Rica, and also recorded observations on roosting and nesting in the Fiery-billed Aracari (*Pteroglossus frantzii*) and the Collared Aracari (*P. torquatus*) in Panama, and a field study of the Keel-billed Toucan in Costa Rica (Skutch, 1958, 1971).

Apparently, little is known about toucans in South America. This study concerns several aspects of the life history of the Red-billed Toucan (*Ramphastos tucanus*) in Guyana, where I conducted field work periodically from May 1964 to August 1966 at Karrow and Akarakuru (Figure 1). I made additional observations at Atkinson Field during 1965 and 1966 and at Karrow and Kibilibiri (Figure 1) during July and August 1971. My studies concentrated on social organization, feeding behavior and foods, vocalizations, and reproductive behavior of unmarked birds.

Distribution and Habitat

Distribution

The Red-billed Toucan ranges over tropical South America from the northern Amazon River basin in Brazil to the coastal Guianas, west through Venezuela to the eastern Andes in Colombia (Meyer de Schauensee, 1966). In Guyana this species is found in primary and secondary forests throughout the country but is especially common in rain, montane, and savanna forests (Figures 1–5). Snyder (1966) states that this species is widespread in Guyana and altitudinally ranges to about 1,437 meters on Ayangana Mountain. At Karrow, Akarakuru, Atkinson Field, and Kibilibiri the Red-billed Toucan is sympatric with the Channel-billed Toucan (*R. vitellinus*), Guiana Toucanet (*Selenidera culik*), Green Aracari (*P. viridis*), and Black-necked Aracari (*P. aracari*).

Habitat

Karrow, Akarakuru, and Atkinson Field (Figure 1) are all located in the sand and clay belt, an area of primary rain forest with small patches of secondary growth. The region is characterized by gently undulating hills varying in relief from 30 to 122 meters (Cummings, 1965). The two dominant soil types at all three locations are a coarse white or podzolic sand known as *Wallaba* sand and a finer grained reddish brown sand with some clay (Hughes, 1947). These soils combined with year-round average annual rainfall of 2,750 millimeters, and an average temperature of 27° C (Akai and Matadeen, 1970) are ideal for mixed forests (Hughes, 1947). Of special interest to this study are the fruits of several tree species belonging to the families Araliaceae, Burseraceae, Chrysobalanaceae, Lauraceae, Meliaceae, Moroaceae, and Palmaceae, which are the main food resources of the toucans.

The trees of the rain forest are evergreens. Some have enormous buttresses supporting extensive canopies over 35 meters high (Figure 2). There are also many tall, straight saplings ranging in height from about 3 to 12 meters. The canopies cast much shade, retarding the growth of green plants on the forest floor. As a result, the only substantial ground cover is a very thin layer of soggy leaves, and most associated plants are aerial and climbing epiphytes of the Araceae, Bromeliaceae, and Orchidaceae families and

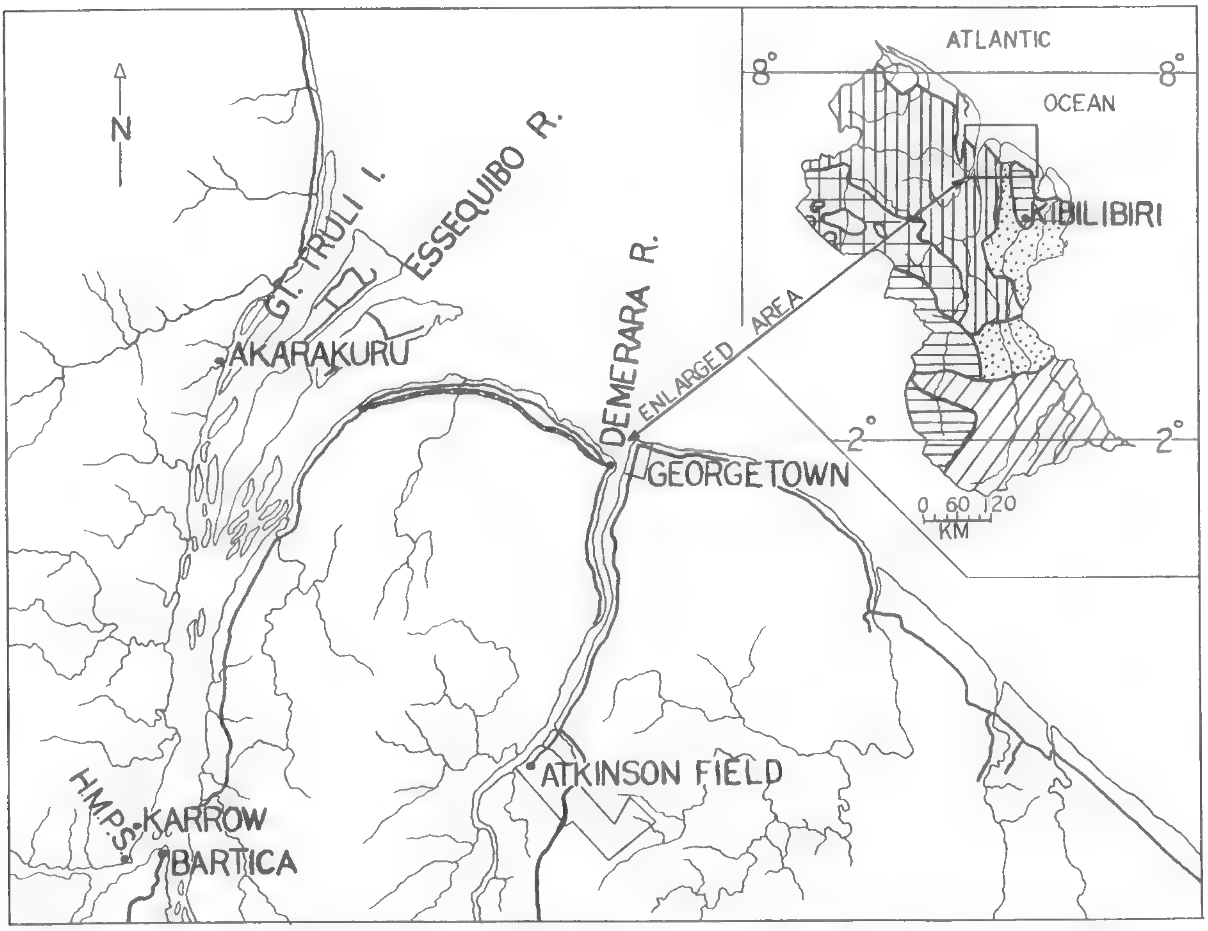

Figure 1. Map of north–central Guyana, showing the locations of the study area. Inset map of Guyana shows the distribution of different forest types: rain (vertical lines), montane-rain (diagonal lines), seasonal (dots), savanna (horizontal lines), and dry evergreen (boxed). The Red-billed Toucan lives in all of these forest communities.

Figure 2. Aerial view of the rain forest at Karrow, showing the extensive canopies in which Red-billed Toucans spend most of their time.

lianas belinging to the Bignoniaceae and Leguminosae families. Parasites of several plant families are also represented and a few ferns are found at lower levels and on the forest floor.

Although Kibilibiri (Figure 1) is also situated in the sand and clay belt, its vegetation is quite different from the rain forest areas of Karrow, Akarakuru, and Atkinson Field. It lies on the eastern edge of the Berbice savannas and is covered by grasses, sedges, scattered bush (especially Sandpaper trees, *Curatella americana*, Figure 3), numerous expanses of bush islands (Figure 4), and fringing forests (Figure 5). The terrain is gently undulating with elevations varying from about 24 to 27 meters above sea level (Myers, 1936). Although Kibilibiri receives an average annual rainfall of 2,250 millimeters (Akai and Matadeen, 1970), savannas predominate.

The bush islands vary from small patches 50 by 80 meters to expanses of woods several kilometers square, always sharply delineated from the savanna. I have found many tree species in bush islands that occur in the rain forest and are used by toucans as food resources. The bush-island forests of Kibilibiri are not so tall as the rain forests of the other study areas. The fringing forests of Kibilibiri consist mainly of rain forest species up to 30 meters in height and clumps of Jauairi Palms (*Astrocaryrum jauari*) and Guava (*Psidium* sp.) growing close to, or in, the water.

Species Description

Cassin (1867), Cleare (1938), Snyder (1966), and Haverschmidt (1968) have published species descriptions of the Red-billed Toucan. The adult's plumage is predominantly black, but the back, rump, wings, and tail have a bluish gloss (color terminology from Grumbacher, 1962). The chin, throat, upper breast, and auriculars are white, faintly tinted with yellow. The lower and upper breast are separated by a narrow dark red pectoral band. The upper tail coverts are light cadmium yellow while the under tail coverts are light cadmium red.

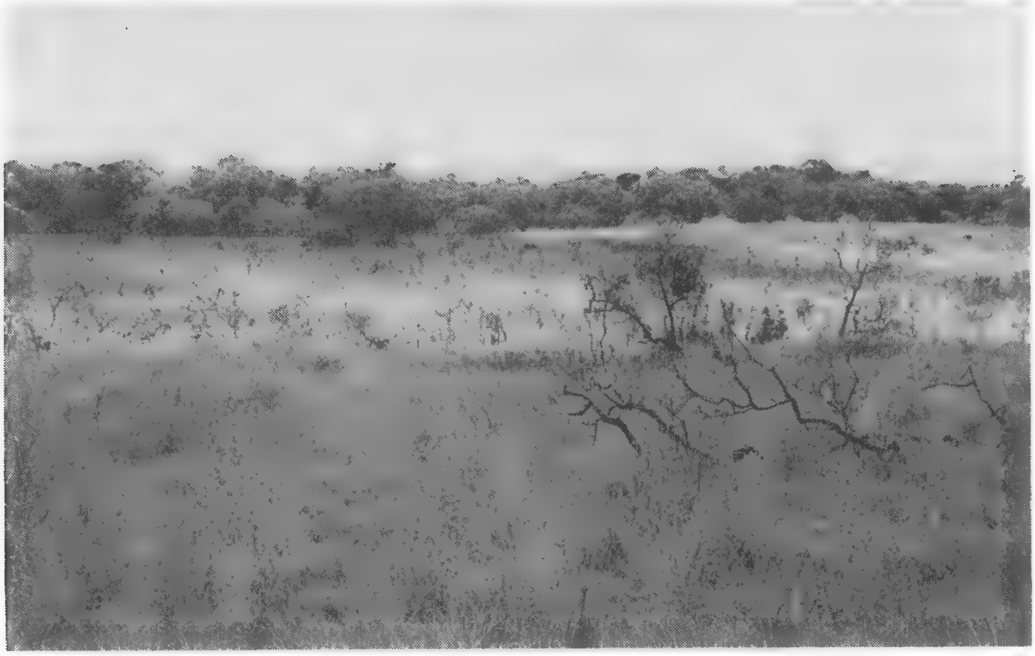

Figure 3. Savanna habitat at Kibilibiri, showing fringing forest where Red-billed Toucans are sometimes found.

The conspicuous, serrate-edged bill is mostly dark alizarine crimson in the majority of individuals, but varies to dark cadmium orange in others. A narrow black band separates the wide yellow band of the maxilla from the red area. The wide base band of the mandible is cobalt blue and separated from the red area by a narrow black band. The bases and the tomia of the maxilla and mandible are black. The naked area around the eyes are cerulean blue; the tarsi and feet are a dark lead-blue. The iris is usually dark brown but I have collected one adult male with yellowish irises.

Juveniles are similar to adults but wear a brownish black plumage that lacks the gloss of the adult plumage. The chin, throat, upper breast, and auriculars are also white but the yellow tinting is less intense. The red pectoral band diffuses more extensively over the black of the lower breast, and the yellow and red of the upper and lower tail coverts are duller. The bill is like that of the adults but with duller red, blue, and yellow areas. The orbital skin is cerulean blue like the adults'; but the tarsi and feet are a darker lead-blue because the scales, or scutes, are black centrally. The iris is a light cobalt blue from about the third week of hatching until the first prebasic molt when it becomes dark brown.

The usually more robust adult males make it quite easy to detect the difference between the sexes in the field, even though the plumages are similar. The extent of this difference is shown by the range of weights listed by Haverschmidt (1968) for birds collected in Surinam — 540 to 690 grams for males and 420 to 514 grams for females. Although I did not weigh the toucans collected, I recorded linear measurements of 12 birds. Five were collected at Akarakuru on 30 August 1964 and seven at Karrow on 14 April 1965. I sexed them all by inspection of the gonads. Measurements were made in inches before skinning and then converted to millimeters. Results (Table 1) reveal some overlap in length, tail, bill, and tarsus measurements, but males tend to be larger than females, supporting the size difference apparent in the field. Although my sample sizes are small, I believe that wing measurements (Table 1) may prove to be the best criterion for sexing Red-billed Toucans.

Systematics

Because an emphasis is placed on bill color in the taxonomy of toucans, there is confusion as to the status of toucans with orange-colored bills. At present, toucans with orange-colored bills enjoy specific status and are called Orange-billed Toucans, *Ramphastos aurantiirostris* (Meyer de Schauensee, 1966). I have treated toucans with orange-colored bills as *R. tucanus.* In Guyana they are sympatric with toucans with red-colored bills. They are members of *Tucanus* flocks and interbreed with the red-billed form. The pair I observed at Karrow from 2 May to 18 July 1964 included a red-billed male and an orange-billed female. Both of their progeny had red-colored bills. My observations suggest that orange-billed individuals are part of the red-billed complex, and that *R. aurantiirostris* should be called *R. tucanus.*

Composition of Flocks

Red-billed Toucans live in year-round flocks, with the members of each group, apparently, jointly defending a home range from adjacent groups. As far as I could determine, most birds were members of a flock, but I observed some single individuals and what appears to be inter-flock transfers. Also, during the breeding season, nesting Red-billed Toucans appear to break away from their flock at least one month before egg-laying to establish their nesting territories. They defended these territories against conspecifics although they seemed to tolerate other toucan species in the nest tree, according to a single observation made at Karrow in April-May 1964. In the Emerald Toucanet, flocks also break up in February, and nesting begins in March, a month later (Wagner, 1944).

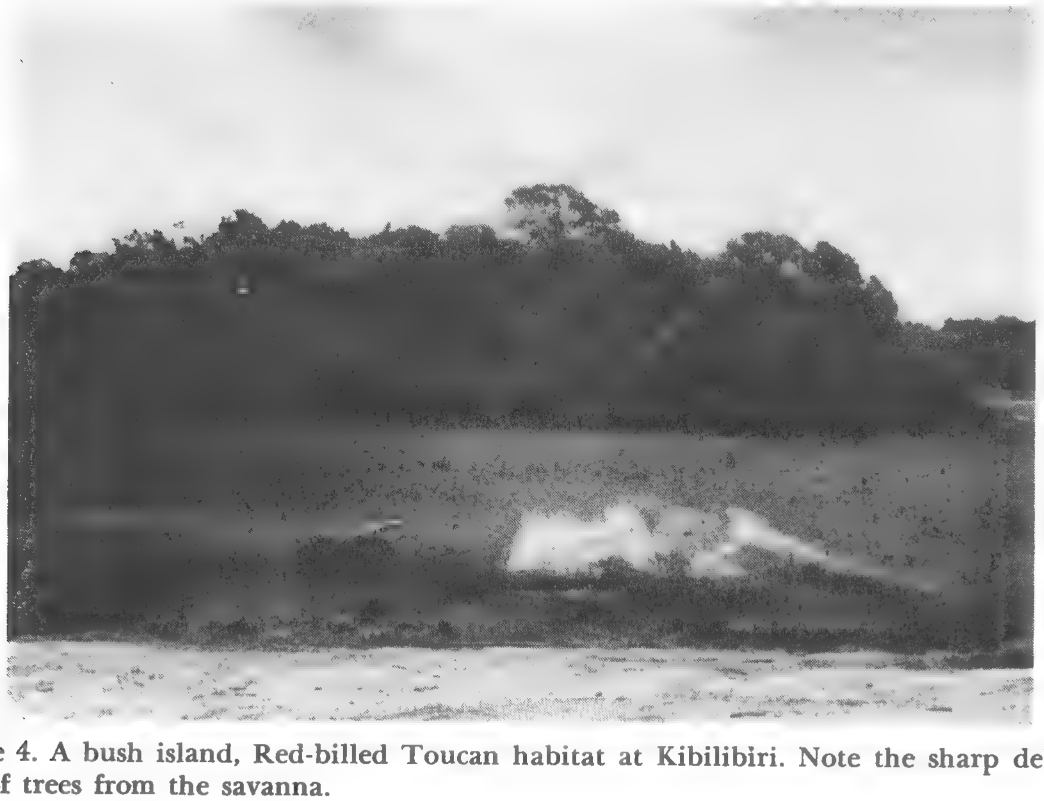

Figure 4. A bush island, Red-billed Toucan habitat at Kibilibiri. Note the sharp delineation of trees from the savanna.

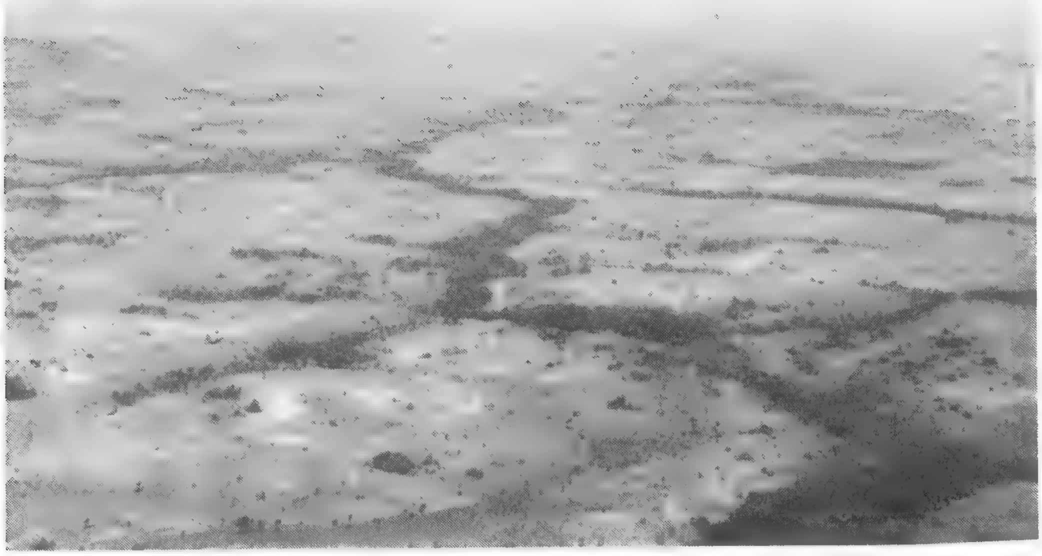

Figure 5. Aerial view of fringing forest habitat in the Rupununi savannas where Red-billed Toucans are found.

Observing five flocks at Karrow and Akarakuru and collecting the members of two flocks, also at Karrow and Akarakuru, suggest that the sex ratio tends to be equal. However, in some flocks males outnumber females. The flock collected at Akarakuru on 30 August 1964 consisted of two adult males, two adult females, and a juvenile male; the flock collected at Karrow on 14 April 1965 consisted of four adult males and three adult females.

Typically, flocks numbered four to six individuals, although one observed at Akarakuru had ten individuals, and one flock at Karrow and two at Atkinson Field had two birds each. During July and August, many flocks had three individuals and, as Beebe *et al.* (1917) stated, probably consisted of adults and their fledgling. During other seasons, toucan flocks may be composed of mated pairs only, or of mated pairs and juveniles, or of mated pairs and single adults. I suspect that most adults were paired, because I observed courtship feeding regularly throughout the year.

Behavior

Courtship Feeding

Observations made from 1964 to 1966 at Karrow, Akarakuru, and Atkinson Field revealed that male birds always initiated courtship feeding, usually without any visible or audible signals from the female recipients. Of 402 recorded instances of courtship feeding in *R. tucanus*, 36 (9 percent) involved an exchange of food by the pair. A typical example of this reciprocal feeding was recorded on 2 April 1965 at Atkinson Field during the late afternoon. As two toucans foraged in a cecropia tree, the male offered a small fruit to the female. The female promptly swallowed it. The male then regurgitated a fruit and presented it to the female in the tip of his bill, but she immediately dropped it. Then she regurgitated a fruit and gave it to the male, which swallowed the fruit.

TABLE 1

Mean Linear Measurements[1] of 11 Adult Red-billed Toucans Collected at Akarakuru and Karrow, 1964 and 1965

Measurement	*Males* (n = 6)	*Standard deviation*	*Females* (n = 5)	*Standard deviation*
Total length	550.2 (547–555)	2.9	543.2 (540–546)	2.4
Tail	138.0 (134–143)	4.7	132.2 (130–135)	1.9
Bill[2]	171.0 (163–179)	6.8	162.4 (160–164)	1.5
Wing[3]	237.5 (235–240)	1.9	219.2 (215–227)	4.8
Tarsus	49.5 (46–53)	2.7	43.2 (40–48)	3.3

[1] All measurements in millimeters.
[2] Exposed culmen.
[3] Flattened.

Courtship feeding appears to be widespread in the Ramphastidae, as I have observed this behavior in the Channel-billed Toucan, Guiana Toucanet, Green Aracari, and Black-necked Aracari. Skutch (1971) reported courtship feeding in the Keel-billed Toucan, Chestnut-mandibled Toucan (*Ramphastos swainsonii*), Fiery-billed Aracari, and the Blue-throated Toucanet.

Billing and Preening

In addition to courtship feeding, I have also seen paired toucans engage in mutual billing (gently touching and nibbling the tips of each other's bills) while perched quite close together. Billing was followed by self-preening or allopreening. Of 81 recorded instances of billing activity, 63 (78 percent) included self-preening, 14 bouts (17 percent) included both self-preening and mutual allopreening, and four bouts (5 percent) consisted of mutual allopreening alone. These billing and preening activities usually took place during the early afternoon (13:00–15:00) as the birds loafed in the trees. Skutch (1972) observed mutual allopreening in mated Chestnut-mandibled Toucans.

Play

I observed periodic bouts of behavior called "play" by Van Tyne (1929). Play included bill-fencing, bill-pushing, fruit-passing, and tagging; descriptions of each of these activities are given below. On 25 August 1965, during the late afternoon, I observed a flock of five toucans at Karrow engage in "play." Two females struck their bills together as if fencing (Figure 6). This lasted about 90 seconds. One of the females hopped toward her mate, striking the branch on which she moved with the sides of her bill, producing a resounding crack with each blow. She then engaged her mate in a fencing bout. After awhile they grasped bills and alternately pushed each other. Soon, however, the female was forced backward to the tip of the branch and had to take flight. She perched a few meters away but the male did not pursue her. During this time the other two males in the flock had initiated a fencing bout.

Sometimes the fencing bouts included passing a fruit. On 29 August 1964 at Akarakuru, I observed two males fencing. During the bout, one toucan regurgitated a green fruit, threw it into the air toward its "opponent," which caught it in its bill. The recipient then bounced away on the branch toward a female and passed the same fruit to her by tossing it into the air. She mandibulated the fruit for a short while, tossed it into the air and another male sitting close by immediately caught it.

I have also seen Red-billed Toucans flying back and forth supplanting members in the flock and, in turn, being supplanted by the displaced bird or by another toucan. The give-and-take between supplanting and supplanted occurs rapidly. This behavior is reminiscent of the game of tag and seems to lack the aggressive components and contact of true supplanting, hency my term tagging.

I observed this play behavior throughout the year. It probably serves to strengthen the bonds between members of the flock. I have also seen play in the Channel-billed Toucan and the Black-necked Aracari. Skutch (1958) described similar behavior in the Fiery-billed Aracari.

Roosting

Toucans apparently roost side by side in close contact with each other, judging from a single observation made at Karrow on 28 August 1965. Two friends and I were censusing Pauraques (*Nyctidromus albicollis*) along a three-kilometer stretch of forest at about 21:00 hours. We used flashlights to illuminate the path and pick out the birds as they sat on the path. I happened to shine my light into the canopy of a kakaralli (*Eschweilera* sp.). After moving the beam around for a short while, I noticed five black silhouettes sitting side by side on a horizontal branch about 22 meters above us and well-protected by overhead foliage. Two of the toucans, disturbed by the light, withdrew their bills from over their backs, looked down for a short time, and resumed their sleeping postures. I checked the same tree for the roosting toucans on 29 and 30 August, but could not locate them.

Concerning the roosting habits of the *Ramphastos* toucans, Van Tyne (1929) believed they roosted in small flocks in tree cavities, based on data provided by natives in Panama. Probably he also was influenced by his sightings of the smaller Collared Aracari roosting communally in an old woodpecker cavity (Van Tyne, 1929). Skutch (1958) reported as many as six aracari toucans roosting in woodpecker holes or natural tree cavities. I observed Black-necked Aracaris and Green Aracaris roosting communally in old Lineated Woodpecker (*Dryocopus lineatus*) and Crimson-crested Woodpecker (*Phloeoceastes melanoleucos*) holes at Karrow; but I have never seen *Ramphastos* toucans roosting in a cavity except during incubation and nestling development, at which time one parent roosts in the cavity. Skutch (1944) always has doubted that the communal cavity roosting habit is practiced throughout the family and concluded that *Ramphastos* toucans roost among foliage (Skutch, 1971). My single observation of roosting Red-billed Toucans supports Skutch's conclusion.

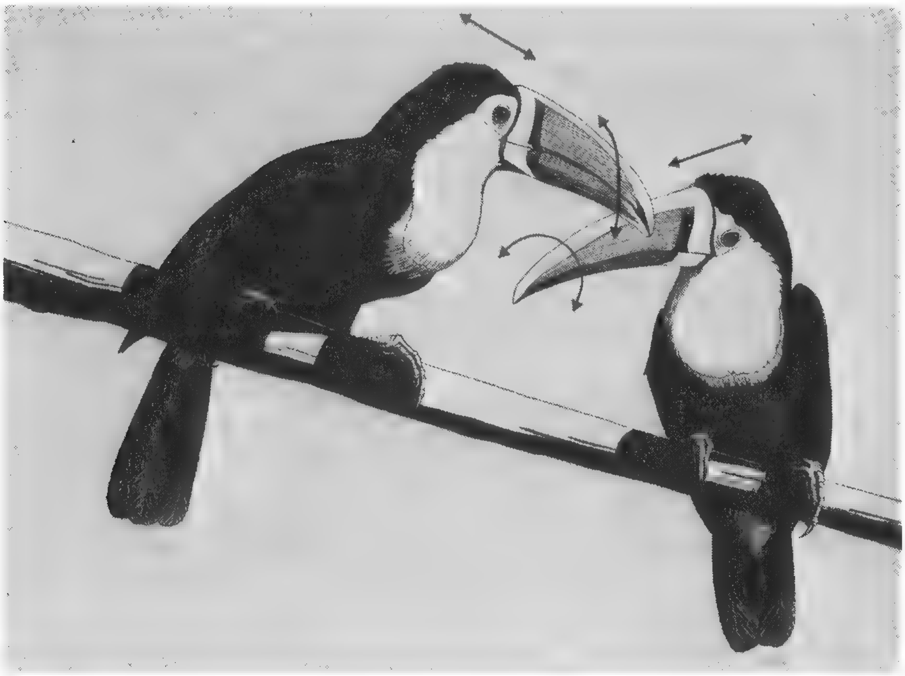

Figure 6. Bill-fencing in Red-billed Toucans is accomplished by a rapid series of side-to-side and forward and backward movements of the head, causing the bills of both birds to make repeated contact.

Van Tyne (1929) and Skutch (1971) published detailed descriptions of the sleeping postures of *Ramphastos* toucans. My observations of toucans maintained in captivity revealed that the Red-billed Toucan turns its large bill over its shoulder and lays the bill on its back so that the mandible nestles among the back feathers. The tail is then tilted forward until it comes in contact with the bill and covers it. All the contour feathers are fluffed so that the bird appears rounded.

Flight

Although Red-billed Toucans appear to form strong pair-bonds and live in flocks, they never fly as a uniform flock. Instead, movement may be initiated by any member of the flock as it flies to another tree not far away. After some time another follows. Soon the others fly one at a time, until the group is reunited at the new location.

The swift, graceful undulating flight of the Red-billed Toucan is produced by a series of three to eight rapid wing-beats, followed by a pause in flapping, at which time the wings are closed. As the toucan goes into a shallow nose dive, the wings are opened immediately, causing it to glide. Then, with rapid wing-beats, the toucan recovers altitude. The toucan's flight pattern is somewhat like that of a woodpecker.

Though graceful in flight, Red-billed Toucans are weak long distance fliers. On 14 August 1964, a friend, Juliet Lowe, picked up a Red-billed Toucan from the Mazaruni River as she was crossing from Bartica to Karrow. She saw the bird attempt to fly across the river from the north to the south bank, a distance of about 3 km. The toucan became exhausted and crash-landed in the river. When I visited Aishalton in the south savannas during April 1966, a Wapisiana Indian told me that they caught toucans by chasing them from bush island to bush island until the birds became exhausted and fell to the ground. Cummings (1965) reported that this type of toucan-hunting occurs during the dry season (October-March) in the Rupununi savannas.

Food and Feeding Behavior

Food

Visual observation suggests that the principal foods of the Red-billed Toucan at Karrow and Akarakuru are the fruits of several species of forest trees, including the warimia (*Tapinia quianensis*), hicha, porobai (*Protium crenatum*), dalli (*Virola surinamensis*), silverballi (*Ocotea* sp.), karohoro or matchwood (*Didymopanax morototoni*), acquero, awarra, and awarraballi (*Astrocaryum* spp.), ulu (*Trattinickia* sp.), congo pump (*Cecropia* sp.), guava (*Psidium* sp.) and the cultivated jamoon (*Syzygium cumini*). These constitute a major part of the toucan's diet.

Inspection of alimentary tracts of the five toucans collected at Akarakuru on 30 August 1964 and the seven collected at Karrow on 14 April 1965 supports these observations. Only two of the birds had cicada remains in addition to fruit fragments in their alimentary tracts; the remainder had only fruit fragments. Earlier reports by Cleare (1938) stated that the principal foods of the Red-billed Toucan in Guyana are fruit, seeds, and nuts, while Smooker (1961) reported a diet of fruit which might be varied by animal protein. More recently, Haverschmidt (1968) recorded fruits and berries as the diet for populations in neighboring Surinam. I occasionally saw individuals take cicadas, beetles, caterpillars, and once an arboreal lizard. Also, on 12 April 1965 at Karrow, I saw a pair of Red-billed Toucans destroy the nest of a Rusty-margined Flycatcher (*Myiozetetes cayanensis*) and swallow three eggs. During this foraging bout, the toucans were mobbed by four Rusty-margined Flycatchers, three Great Kiskadees (*Pitangus sulphuratus*), and five Tropical Kingbirds (*Tyrannus melancholicus*). Smooker (1961) reported a similar incident in which a single toucan destroyed an empty nest while being mobbed by Rusty-margined Flycatchers and Great Kiskadees.

Feeding Behavior

Foraging activity of the Red-billed Toucan can be conveniently studied by observing a fruiting tree in a clearing, especially during the three hours after sunrise. The flock straggles in across the clearing, one member at a time. As soon as each toucan arrives, it approaches the fruit at the branch tips by a series of swift, long bouncing leaps. Then, perching at bill length from a bunch of fruit, it seizes an individual fruit between the tips of its bill. If this initial seizure does not dislodge a fruit, a lateral twist of the head usually procures it. Sometimes the fruit is held at the tip of the bill, juggled for a while, then swallowed by tossing the head backward and simultaneously opening the bill, catching the fruit in the throat. Large fruit and catkins are sometimes held against a perch with one or both feet as pieces are torn off with the bill, but most fruit is swallowed whole.

When foraging for animal food, the toucan perches and moves its head slowly and deliberately, at the same time turning it at odd angles as it inspects foliage, twigs, and branches. Animal food items are seized between the tips of the bill, then struck against the perch before being swallowed whole. Large cicadas, after being subdued, are held against the perch by both feet and torn apart.

Although Red-billed Toucans generally feed in the canopy, they descend to lower levels to feed on ripe fruit and animal food items that might be found there. I never saw them take fallen fruit off the forest floor as Lill (1970) reported for the Channel-billed Toucan.

Interactions at Fruiting Trees

Early in this study, I noticed that fruiting trees attracted toucans and several other species and that these foraging congregations exhibited much inter- and intra-specific interaction. I therefore studied avian visitors to an individual warimia tree at Akarakuru from 5 to 11 August 1964 for a total of 42 hours between 06:00 and 12:00. The warimia tree was on the edge of a recently cleared second-growth area. This tree was 14 meters tall and its sparsely leafed crown permitted easy observation of its avian exploiters. Warimia fruits are green, ovoid drupes (14 mm × 9 mm) that grow in compact clusters.

Toucans exploited the fruit more than any other group (Table 2), with the Red-billed Toucan making the most feeding visits. Only 12 of the 27 species were represented by more than one individual at any given time in the fruit tree; these species included the parrots, toucans, Yellow-tufted Woodpecker (*Melanerpes cruentatus*), and Cayenne Jay (*Cyanocorax cayanus*), all flocking species; whereas the Blue-gray Tanager (*Thraupis virens*) and Palm Tanager (*T. palmarum*) visited in pairs or trios.

Of the 15 species that interacted with the Red-billed Toucan (Table 2), only a single large Channel-billed Toucan was successful in supplanting Red-billed Toucans. There were more cases of inter-specific (186) than intra-specific (15) encounters for the Red-billed Toucan. Of the 201 recorded encounters, only 20 caused supplanted individuals to leave the tree. In the remaining 181 encounters, the supplanted individuals moved to another part of the tree and continued to feed.

Vocalizations

Toucans are not known for their quality of voice (Skutch, 1971). The Red-billed Toucan is not an exception, but is probably the best vocalist of the toucans found in Guyana. Both sexes vocalize, mostly at sunrise and to a lesser extent at sunset or just before a rain storm. In June and July 1971, I recorded 63 songs of 13 Red-billed Toucans at Karrow. The recordings were made on a Uher 4000 Report L tape recorder using a tape speed of seven and one-half inches per second. The standard Uher microphone was mounted in a 25-inch diameter parabola. Songs were graphed on a Kay Electric Company Vibralyzer at the wide band setting.

From a distance, the song of the Red-billed Toucan sounds like the yelping of a puppy, with a hollow, throaty quality. The song can be phoneticized: *yeock yook yook yeock yook yook yook*, in a seven-note version. The number of notes in a song varies from four to sixteen. The songs of any given toucan also show some variation of patterns. Of the three basic

TABLE 2

Species Observed Feeding on the Fruit of a Warimia Tree and the Number of Times Supplanted by Red-billed Toucans at Akarakuru from 5 to 11 August 1964

Species	*No. of feeding visits*	*No. of times supplanted by Red-billed Toucans*
Lilac-tailed Parrotlet (*Touit batavica*)	13	3
Black-headed Parrot (*Pionites melanocephala*)	43	0
Dusky Parrot (*Pionus fuscus*)	7	0
Orange-winged Parrot (*Amazona amazonica*)	46	0
Black-tailed Trogon (*Trogon melanurus*)	30	4
Black-spotted Barbet (*Capito niger*)	15	9
Red-billed Toucan (*Ramphastos tucanus*)	147	15
Channel-billed Toucan (*R. vitellinus*)	92	34
Black-necked Aracari (*Pteroglossus aracari*)	132	15
Guiana Toucanet (*Selenidera culik*)	75	10
Lineated Woodpecker (*Dryocopus lineatus*)	43	2
Yellow-tufted Woodpecker (*Melanerpes cruentatus*)	78	0
Black-tailed Tityra (*Tityra cayana*)	80	21
Crimson-hooded Manakin (*Pipra aureola*)	36	0
White-bearded Manakin (*Manacus manacus*)	20	0
Tropical Kingbird (*Tyrannus melancholicus*)	30	0
Rusty-margined Flycatcher (*Myiozetetes cayanensis*)	24	0
Great Kiskadee (*Pitangus sulphuratus*)	19	0
Cayenne Jay (*Cyanocorax cayanus*)	8	5
Pale-breasted Thrush (*Turdus leucomelas*)	30	0
Bare-eyed Thrush (*T. nudigenis*)	21	11
Violaceous Euphonia (*Euphonia violacea*)	80	0
Blue-gray Tanager (*Thraupis virens*)	94	10
Palm Tanager (*T. palmarum*)	88	17
Silver-beaked Tanager (*Ramphocelus carbo*)	58	19
White-lined Tanager (*Tachyphonus rufus*)	46	2
Buff-throated Saltator (*Saltator maximus*)	21	14

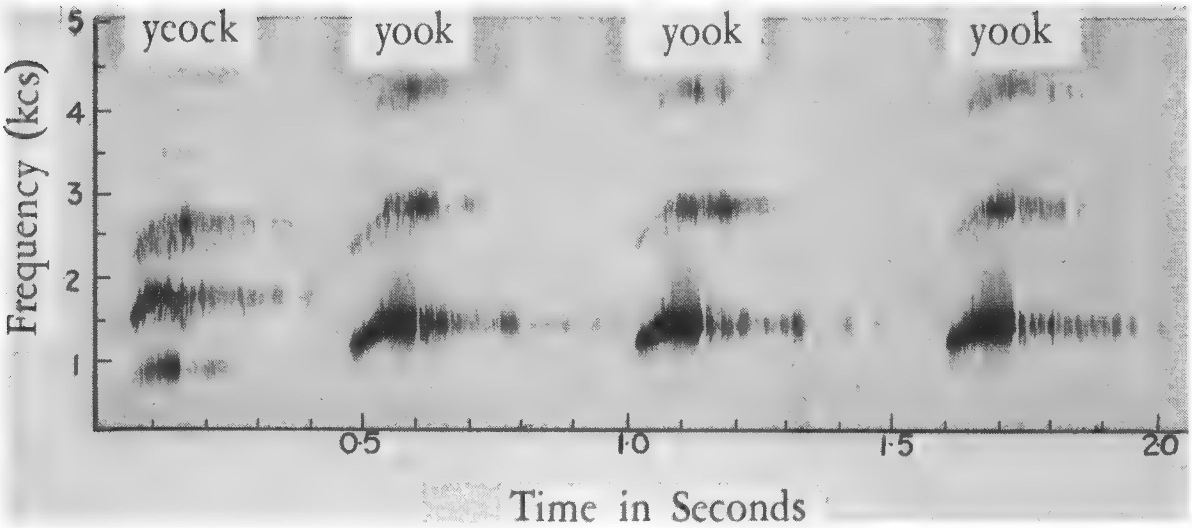

Figure 7. Sound spectrogram of the vocalization pattern of a male Red-billed Toucan.

notes, *yook, yeock* (Figure 7), and *yee-ock* (Figure 8), the *yook* note is used most frequently. Typically, three, four, or five *yook* notes are separated by a *yeock* or *yee-ock* note. I have no recordings with both *yeock* and *yee-ock* notes in the same song. The song may begin or end with any one of the three notes.

The *yeock* note is pitched lower than both the *yook* and disyllabic *yee-ock* notes (Figures 7 and 8) and is also of shorter duration than the *yook* note (Figure 7). The *yook* note is not steady in pitch but begins at about 1 kilocycle per second and slurs up to about 1.5 kcs (Figures 7 and 8), where it levels off. This note also breaks up toward the end of the delivery. Donald Borror (pers. commun.) suggests that this may be due to sound energy bouncing off foliage, producing an echo effect. The *yee-ock* note begins at about 1.2 kcs, sliding up to 1.8 kcs, then down to about 1.2 kcs, and finally up to about 1.5 kcs, where it levels off in pitch (Figure 8). Each note has at least two harmonics (Figures 7 and 8).

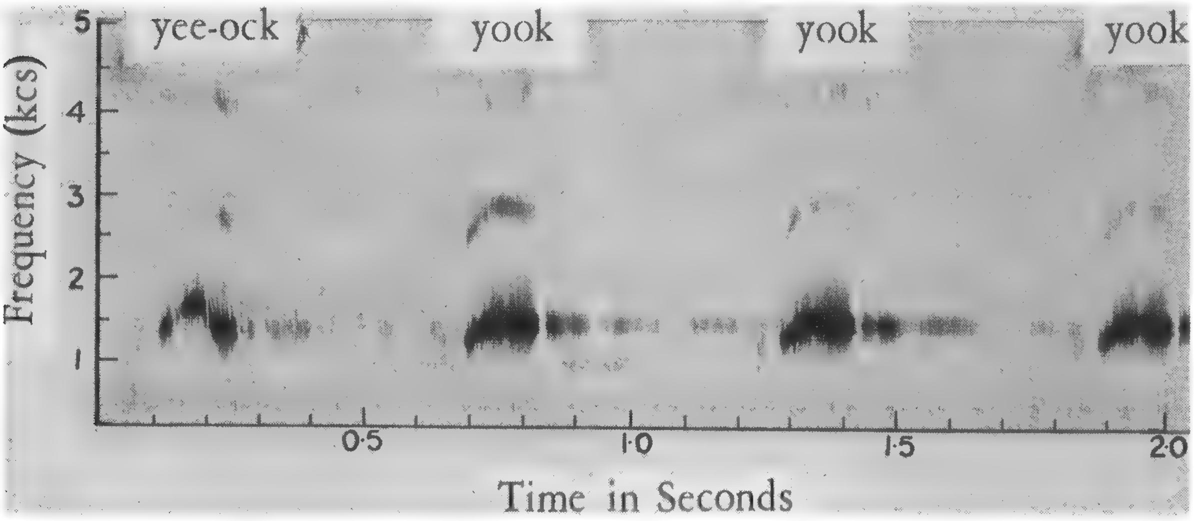

Figure 8. Sound spectrogram of the vocalization pattern of a female Red-billed Toucan.

The toucans deliver these vocalizations from exposed tree crowns. The great amplitude of the notes and the exposed singing perches make these birds very conspicuous. In singing, and sometimes in calling, the head is tossed laterally and up and down, and the tail is jerked violently upwards with each up-toss of the head. At the same time, the bird sways from side to side in a jerky animated motion.

Red-billed Toucans are most vocal from March to July, which coincides with the peak nesting season (Beebe *et al.*, 1917; Cleare, 1938; Bourne, pers. observ.); however, singing also occurs during other parts of the year.

Skutch (1971) found that Keel-billed Toucans used the same notes in singing as in protesting human presence at their nest. I found this to be true of the Red-billed Toucan. In their protest calling, they used two, three, or four notes and it was usually the *yook* note. This vocalization was also used when a troop of Capuchin monkeys (*Cebus capucinus*) robbed a toucan nest on 28 June 1971 at Karrow.

During nesting, and sometimes during courtship feeding and intra- and inter-specific agonistic encounters, toucans produced a vocal castanet-like rattle of short duration. Van Tyne (1929) and Skutch (1971) both observed this as part of the vocal repertoire of Keel-billed Toucans. Van Tyne (1929) stated that this mechanical rattle was used frequently around the nest and also was produced by captive birds. I have heard the rattle vocalization in captive Red-billed Toucans. Skutch (1972) reported that the Chestnut-mandibled Toucan gave the rattle vocalization while defending its nest from a small mammal.

Breeding

My observations suggest that at least one, but not all, of the pairs in a flock produce clutches in a given breeding season. Apparently, conspicuous courtship does not occur in this species and actual mating is brief. Neither Van Tyne (1929) nor Skutch (1971) has described courtship for the Keel-billed Toucan, which supports my observation that conspicuous courtship is absent in this genus. However, I observed the mating of the Red-billed Toucan on one occasion. While watching a group of five toucans foraging at Karrow on 15 December 1965 at approximately 08:00, I noted that two of the birds were engaged in courtship feeding. Then, quite suddenly, the male mounted the female, which by that time held the wings slightly open and in a drooped position. The male made a few treading movements while thrashing the air with his wings. The female ruffled her contour feathers and elevated her tail. After the male lowered his fanned tail, he shoved forward five times. Each shove was accompanied by a side-to-side wag of his tail. The male then hopped off the female's back and perched on a branch about one meter away. Both birds shook their feathers and preened before flying to another tree about 200 meters away to join the other members of the group. About 35 seconds had elapsed from mounting to dismounting.

Nests and Nest Histories

I observed five active nests at various stages of the nesting cycle at Karrow from 1964 to 1966 and during the summer of 1971 (Table 3). The entrances to the nests, all in natural cavities of living trees, were knotholes

TABLE 3

Measurements of Red-billed Toucans' Nests in Natural Tree Cavities

Date	*Number of nest*[1]	*Height (m) above ground*[2]	*Cavity entrance*[3] *(mm)*	*Cavity depth*[4] *(mm)*	*Tree species*	*Reference*
6 April 1964	1	3.0	150 × 165	560	hicha	Bourne
20 May 1965	2	20.0	64 × 123	603	*Eschweilera* sp.	Bourne
10 June 1965	3	1.3	130 × 162	394	*Inga* sp.	Bourne
28 July 1966	4	14.0	79 × 134	1,200	*Caryocar* sp.	Bourne
26 June 1971	5	9.0	94 × 150	293	*Mora* sp.	Bourne
1917		12.0	72 × 154	900	—	Beebe *et al.*
1938		9–12	64 × 123 to 150 × 165	—	—	Cleare

[1] Nest 1 — found before egg laying; Nest 2 — found with three nestlings about 10 days old; Nest 3 — found with two nestlings about 25 days old; Nest 4 — found with two nestlings about 40 days old; Nest 5 — found with two nestlings about 35 days old.

[2] From ground level to the lower rim of the cavity entrance.

[3] Short and long diameters.

[4] From the lower rim of the entrance to the cavity floor.

TABLE 4

Diurnal Incubation Rhythm of a Pair of Red-billed Toucans at Karrow, 1964

Date observed	*Time observed*	*Total hours observed*	*Attentiveness in minutes*		*Inattentiveness in minutes*		*Constancy percentage*	*Total percent incubation*	
			Range	*Mean*	*Range*	*Mean*		*Male*	*Female*
6 May	05:45–14:09	8.4	3–165	48.8	0–185	34.7	58.4	9.6	90.4
7 May	06:00–10:18	4.3	4–32	17.6	0–81	16.6	51.5	42.3	57.7
8 May	13:00–15:30	2.5	5–34	19.7	0–21	5.7	77.6	50.8	49.2
9 May	08:00–12:00	4.0	2–69	28.5	0–61	11.5	71.3	32.2	67.8
10 May	14:00–16:06	2.1	6–81	36.7	1–8	5.3	87.4	26.4	73.6
11 May	06:00–08:42	2.7	20–45	34.8	0–23	6.3	84.7	34.5	65.5
14 May	05:45–17:45	12.0	15–80	38.9	2–20	8.1	81.8	31.7	68.3
16 May	05:45–17:45	12.0	18–76	37.6	0–19	5.4	83.5	43.6	56.4
18 May	12:00–15:43	3.8	7–103	38.6	0–25	7.0	84.7	30.6	69.4
20 May	07:00–09:24	2.4	28–56	38.3	0–20	9.3	80.5	27.0	73.0
21 May	08:00–11:18	3.3	6–34	24.3	6–50	25.0	49.3	48.4	51.6

and appeared to have been formed as a result of branches breaking off, with weather and fungus decaying the central portion of the tree trunk. The somewhat cylindrical cavities thus formed were used by the toucans for nesting.

None of the observed nests was lined. Eggs were laid on the cavity floor or on regurgitated seeds that were allowed to accumulate in the cavity. Apparently, breeding toucans attempt to enlarge and clean out cavities before laying their eggs. I arrived at this conclusion after observing a pair (Nest 1, Table 3) remove decayed wood and seeds from the nest cavity on 2 May 1964. The removal of seeds from the cavity indicates the cavity probably was used previously for nesting. Nest measurements show that nest entrances varied in height above ground from 1.3 meters to 20 meters (Table 3).

Of the five nests I observed, only Nest 1 was successful. It was found by Levi Lowe on 6 April 1964 before egg-laying; two young fledged between 6 and 10 July 1964. Nest 2 was discovered on 20 May 1965, with three nestlings whose ages I estimated to be about ten days. This nest was presumably destroyed by predation on 24 May 1965. I found Nest 3 on 10 June 1965 with two nestlings about 25 days old. These nestlings disappeared between 15 and 18 June 1965. I found Nest 4 on 28 July 1966 with two nestlings about 40 days old. One nestling disappeared on 29 July 1966 and the other was taken by an unknown predator on 3 August 1966. I found Nest 5 with two nestlings about 35 days old. Capucin monkeys destroyed this nest at 07:05 on 28 June 1971.

Eggs and Clutch Size

On 2 May 1964 I drilled two observation holes in the trunk of the hicha tree, one about 63 mm above the other. I then plugged the holes

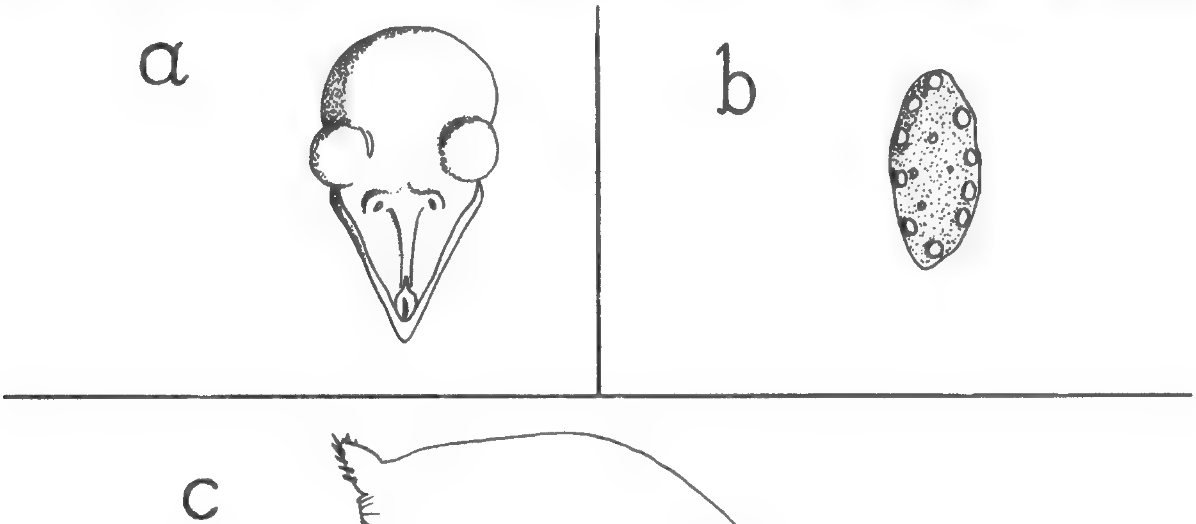

Figure 9. Red-billed Toucan: (A) head of a day-old nestling viewed from above, showing the projecting mandible and egg-tooth at the tip of the maxilla; (B) heel-pad viewed from below; (C) nestling, four days old.

with cork stoppers. When I needed to check on the contents of the cavity, I passed a small electric bulb through the upper hole and observed through the lower one. A bird blind of coconut palm fronds was also constructed about four meters from the cavity entrance. The blind was necessary because Red-billed Toucans are wary nesters and refuse to approach their nests when they detect humans nearby.

On 4 May the female, which was smaller than the male and had an orange bill, spent much time in the nest cavity. On two occasions the male brought food to her which she took at the nest entrance. Both toucans produced the castanet-like vocalization during these courtship-feeding sequences. Both birds took brief turns in the cavity during the afternoon but no eggs were laid before 18:38, when I left the blind. On 5 May at 12:00, I found the first egg, which was laid sometime between 09:00 and 12:00. The second egg appeared after 11:30 and before 14:00 on 6 May.

Clutch and brood sizes varied, with two eggs or nestlings in four nests and three nestlings in one nest (Table 3). Beebe *et al.* (1917) and Cleare (1938) both recorded two-egg clutches for this species. Detailed descriptions of the eggs of Red-billed Toucans have been published by Beebe *et al.* (1917). The eggs were pinkish white and of the general shape of a hen's egg. I did not see the grooves described by Beebe *et al.* (1917).

Incubation and Attentive Periods

I concluded that incubation began with the laying of the first egg on 5 May because both birds regularly spent short intervals in the cavity, the longest being about 20 minutes in duration. Then, at 17:35 on the same day, the male entered the cavity and was still inside the nest when I left the blind at 18:45. The male toucan apparently did all of the night incubating. On 6 May I arrived at the blind at 04:50; nothing happened until 05:38 when the male appeared at the nest entrance, looked about, and then withdrew. At 05:45 the female began calling from a nearby tree top and the male departed. The toucans left the nest by climbing the tangled lianas, progressing by a series of leaps and bounds to the uppermost branches before flying off. Both birds ignored the cavity for three hours that morning although they remained close to the nest site for most of the time. The female approached the cavity at 08:45, looked in five times and left. She returned at 08:55, perched and looked about from high in the nest tree, then descended the tangled creepers by short flights, leaps, and bounds to perch on the stump above the entrance. She looked around in characteristic toucan manner, peering up and down, side to side, slowly, deliberately. Next she hopped onto the entrance rim, paused to look about with her bill projecting into the cavity, then entered the nest. This turned out to be the pattern of approach to the nest by both sexes.

I made periodic observations of the pair's incubation rhythm from 6 to 21 May for a total of 57.5 hours, and used Skutch's (1962) formula for constancy of incubation to calculate the percentage of time the toucans were on the nest. Attentive periods were shorter during the first four days of incubation, ranging from a mean of 17.6 to 48.8 minutes for the periods

TABLE 5

Diurnal Brooding Rhythm of a Pair of Red-billed Toucans at Karrow, 1964

Date observed	*Nestling age in days*	*Time observed*	*Total hours observed*	*Brooding sessions in minutes*		*Non-brooding sessions in minutes*		*Constancy percentage*	*Total percent brooding*	
				Range	*Mean*	*Range*	*Mean*		*Male*	*Female*
22 May	0	06:02–09:26	3.4	13–46	27.7	36–43	39.7	41.1	44.6	55.4
26 May	4	07:05–11:05	4.0	15–38	26.5	5–55	33.5	44.2	54.7	45.3
31 May	9	06:30–11:30	5.0	14–50	31.5	23–80	43.5	42.0	38.1	61.9
5 June	14	13:00–17:18	4.3	10–36	22.3	31–51	42.5	34.4	51.7	48.3
25 June	34	06:30–11:30	5.0	15–28	21.5	109–148	128.5	14.4	34.9	65.1

of observation (Table 4). The long attentive period of 165 minutes on 6 May caused the high mean value for that date and I suspect that it was due to the laying of the second egg. Throughout the incubation period, the shortest attentive periods occurred during the early morning hours. The constancy percent (Table 4) fluctuated daily, and showed a tendency to increase as the incubation period progressed, but suddenly dropped off to 49.3 percent of 3.3 hours on 21 May. I believe that this was due to the hatching of one egg during the mid-afternoon of 21 May and could be attributed to the "restless and agitated" behavior of the parent birds on that date.

I recorded several attentive periods of over 80 percent (Table 4). According to Skutch (1971), a 70-percent attentive period for 11 hours in the Keel-billed Toucan is about normal for the Ramphastidae. However, Skutch (1944, 1967b) also recorded 73.9 percent of 6 hours and 78 percent of 13.5 hours for the Blue-throated Toucanet.

One egg hatched on 21 May. I discovered the nestling when the female left the nest at 16:00 with an eggshell fragment held in the tip of her bill. When I looked into the cavity, the nestling was wet and the other egg was already pipped. Both the hatched and unhatched young were producing a continuous high-pitched, squeaky buzz. On checking the nest on 22 May at 05:02, I found two nestlings and only one small eggshell fragment.

I did not know the precise times of laying and hatching; therefore, computation of the incubation period allows for the determination of a margin of error. Since the last egg (second) of the clutch was laid after 11:30 and before 14:00 on 6 May, I divided the difference by two to determine the margin of error (1 hr, 25 min plus 11:30 = 12:55). The last egg hatched after 18:00 on 21 May and before 05:00 on 22 May, so that the hatching times were treated in the same manner, placing the interval during which hatching occurred at 23:30 (±5.5 hours). Therefore, the incubation period extended from 12:55 on 6 May to 23:30 on 21 May, or 15.5 days (±6.75 hours, the sum of two margins of error). Assuming that the first egg laid was the first hatched, the incubation period was 15.3 days ± 2 hours. Skutch (1944) recorded 16 days for the Blue-throated Toucanet, the only other published record of an incubation period for the Ramphastidae.

Nestlings

At the time of hatching, the pink-skinned toucan is completely naked. The prominent eyes and auditory meatuses are tightly closed. The head is relatively large with a short, broad, heavy bill, the wider mandible being longer than the narrower maxilla, at the tip of which is an egg tooth (Figure 9a). The young toucan also possesses prominent heel-pads. The articulation between the tibiotarsus and the tarsometatarsus is covered by a well-developed, oval, thick horny pad with a ring of nine or ten light-colored protuberances on its periphery (Figure 9b). These pads and the abdomen help to support the weight of the nestling. Because heel-pads make contact with the rough cavity floor, they probably protect the fragile feet from damage.

I recorded the development of the nestlings periodically. Both nestlings were about the same size and developed slowly at about the same rate. By 26 May, when four days old, the nestlings had increased in size and were able to sit up for short periods, but still spent most of the time

TABLE 6

Feeding Rates of a Pair of Red-billed Toucans at Karrow, 1964

Date observed	*Nestling age in days*	*Time observed*	*Total hours observed*	*Number of feeding trips and total percentage*				*Feeding rate in trips per hour*
				Male		*Female*		
22 May	0	06:02–09:20	3.3	1	16.7	5	83.3	1.8
26 May	4	07:05–11:05	4.0	6	40.0	9	60.0	3.8
31 May	9	06:30–11:30	5.0	8	53.3	7	46.7	3.0
5 June	14	13:00–17:18	4.5	9	45.0	11	55.0	4.7
25 June	34	06:30–11:30	5.0	11	50.0	11	50.0	4.4
30 June	39	12:00–17:00	5.0	15	46.9	17	53.1	6.4
5 July	44	08:05–11:05	3.0	9	52.9	8	47.1	5.7

lying on the cavity floor with their heads rolled over on one side. Pinfeathers were visible under the skin and the ten tail feathers projected as a row of small spikes from the uropygium (Figure 9c). By the ninth day (31 May), body size had increased, but there were no visible changes in pinfeather development. By the 14th day (5 June), the maxilla was as long as the mandible and the bill was beginning to look toucan-like. The feather tracts were well delineated and the pinfeathers of the wing coverts were conspicuous. The nestlings' eyes began to open on the 19th day (10 June) and their vocal repertoire included a wail in addition to the squeaky buzz. Each nestling by then was flapping its wings vigorously. Contour pinfeathers had broken through the skin. At 24 days of age (15 June) both nestlings thumped on the cavity floor with their heel-pads and wailed whenever I looked in. They kept their eyes closed whenever I illuminated the cavity. The remiges were long and completely sheathed. On the 29th day (20 June) the nestlings began to exhibit fear reaction by crouching but kept their eyes open for the first time throughout the observation period. A crest of pinfeathers projected through the skin on top of the head. The remiges and coverts were exposed from the tips of their sheaths but the body was still covered by short sheathed pinfeathers. The bill had become more keeled. On the 34th day (25 June) the nestlings were fully feathered; only then did the rectrices begin to show visual development. The color pattern of the bill was like that of the parents and the irises were a light cobalt blue. Each nestling exhibited its first exploratory behavior by pecking at the small electric bulb used to illuminate the cavity. On the 39th day (30 June) the nestlings were looking out of the cavity entrance but withdrew as I approached the nest tree. My visit on the 44th day (5 July) was the last time I saw the nestlings in the cavity; they were about the size of their parents but with smaller bills. On the 49th day (10 July) the nest cavity was empty; on checking the neighboring tree tops, I saw the male feeding one fledgling while the other begged for food. I suspect that fledging took place when the nestlings were 48 or 49 days old because I sighted them in a tree top only 10 meters from the nest tree at 07:30. There are no complete records for nestling period in *Ramphastos* toucans, but Van Tyne (1929) estimated a nestling period of 45 days for the Keel-billed Toucan. Skutch (1971) calculated at least 47 days for the same species. Lill (1970) estimated a minimum of 44 to 45 days and a maximum of 50 to 51 days for the Channel-billed Toucan.

I also observed parental behavior during nestling development. After each observation period of the nestlings, I concealed myself in the blind and my assistant served as a "walk away." The parents then stopped their protest calling and resumed normal behavior. Both parents brooded the nestlings quite often during their first two weeks. A typical brooding rhythm for that period was recorded on 31 May when the nestlings were nine days old (Table 5). Four sequential brooding periods between 06:30 and 11:30 lasted for 28, 34, 50, and 14 minutes, respectively. Thus the toucans brooded for 42 percent of five hours. When the nestlings were 34 days old, the parents brooded for 15 and 28 minutes between 06:30 and 11:30, for 14.4 percent of five hours (Table 5). After the nestlings were two weeks old, the only diurnal brooding recorded was during rain showers. Although both sexes shared brooding at night, I recorded only three night sessions for the female and 12 for the male.

Although both sexes fed the nestlings, they never arrived at the nest simultaneously. The female made most of the feeding trips during nestling development (Table 6). On most of the feeding trips, the parents carried food items in the tip of the bill. Most of the food consisted of fruit (123 trips); but I recorded cicadas on five occasions, caterpillars on four, and a locust and a lizard on one each. The approach of an adult to the nest elicited from the young the wail vocalization which was audible at a distance of about 12 meters. On several feeding trips the adults went into the cavity with food items visible in their bills, emerged with empty bills, regurgitated a fruit and carried it into the cavity. On 5 June at about 09:00 the male repeated this process five times before finally emerging with a bill full of fecal sacs.

Some feeding bouts were intensive. On 25 June the adults fed the young toucans at a rate of seven times in 20 minutes, while on 31 May the feeding rate was once in 2.5 hours. Generally, the feeding rate increased as the young toucans aged; on 22 May when the nestlings were zero days old, the rate was 1.8 times per hour compared to 5.7 times per hour on 5 July when the chicks were 44 days old (Table 6). From the time the nestlings were 39 days, they were fed at the cavity entrance by both adults. After the fledging of the chicks neither the adults nor the young showed interest in the nest.

Discussion

Flock Cohesion

According to Hediger (1950) flocks may maintain cohesion through social mechanisms that include either contact or distance. In the former, the organisms maintain touch-contact with each other, especially when resting (Hediger, 1950); in the latter, animals may come in contact with each other rarely and maintain individual distances between themselves. This study suggests the possibility of both social mechanisms interacting to maintain group cohesion in the Red-billed Toucan.

The mechanism of contact was clearly manifested through body contact by all members of a flock during roosting. The only other time members of a flock may be in touch-contact is during periodic bouts of bill fencing. At other times, only mated pairs touch each other, during mutual billing, allopreening, or courtship feeding. All other flock activities appear to be dependent on distance, especially when foraging and loafing. However, at these times paired birds tend to forage and perch in close proximity to each other.

Flocks are maintained year-round by the Red-billed Toucan, even through the peak breeding season which extends from March to July. It appears that breeding Red-billed Toucans break away from their flocks to establish nesting territories, as the pair studied in 1964 entered the nest cavity at least a month before egg-laying. Some species of toucanets also break away from their flocks. At least three weeks of territorial activity elapsed before Blue-throated Toucanets laid eggs in a hole they had inspected earlier (Skutch, 1944). Wagner (1944) documented the breakup of Emerald Toucanet flocks a month before egg-laying. No helpers were observed for any of the toucanets or for the Red-billed Toucans at the five nests I studied.

At present nothing is known about the age structure of the flocks of Red-billed Toucans, or of the relationship of their age to breeding. Since most members in a flock appear to be paired, a long period of pair-bonding might be necessary before birds can breed. Skutch (1958) believes that Fiery-billed and Collared Aracaris do not breed before they are about two years old. A similar situation might exist in Red-billed Toucans.

Billing and Courtship Feeding

Billing and courtship feeding are important behaviors in maintaining social organization in the Red-billed Toucan. Several hypotheses have been developed to explain the significance of courtship feeding. According to Armstrong (1965), billing and courtship feeding are related, both having evolved from the mechanics associated with the feeding of young birds. Thus gaping and reaching for food became ritualized as adult sexual displays. He also suggested that many species which bill also feed their mates during courtship or incubation. Lack (1940) considered courtship feeding important in maintaining the pair-bond. Later, Lack (1966) discarded his earlier hypothesis because he was impressed by the amount of food given to the female. He identified the survival value of courtship feeding, therefore, as supplying the female with additional energy for the formation of eggs (Lack, 1968), a view also held by Balda and Bateman (1972). In the Great Tit (*Parus major*), courtship feeding by males supplied the females with about a third of their daily intake of food during the courtship period (Royama, 1966). Balda and Bateman (1972) found a similar situation in Piñon Jays (*Gymnorhinus cyanocephalus*).

I suspect that courtship feeding in the Red-billed Toucan serves largely to strengthen and maintain the pair bond rather than serving as a mechanism for obtaining additional food for egg-laying. This conclusion is based on the following observations: (1) Courtship feeding was a year-round activity. (2) Most courtship feeding occurred while the flock foraged, so that the females probably obtained all the food they needed on their own. In fact, on several occasions the females dropped the food presented to them by the males. (3) Females sometimes fed males.

Billing in the Red-billed Toucan appears to be of two types. One form, engaged in by mated birds only, includes gentle touching and nibbling of the tips of each other's bills; whereas the other, bill fencing, is engaged in not only by mated birds but also members of flocks. In bill-fencing, the participants strike their bills together. Van Tyne (1929) interpreted this as "play" and Armstrong (1965) believed that it was probably a ritualization of aggression.

Play

Marler and Hamilton (1967) found that most observers regarded certain behaviors as play because, in their judgment, the behaviors lacked "seriousness." The Red-billed Toucan's behavioral repertoire includes bill-fencing, bill-pushing, tagging, and fruit-passing, behaviors which at the time I observed them appeared to serve no immediate function, except, as Armstrong (1965) suggested, to expend surplus vitality. I therefore categorized these behaviors as play as did Van Tyne (1929) for the Keel-billed Toucan.

Play is widespread among birds (Nice, 1962; Thorpe, 1956). Recently, Kilham (1974) documented play behavior in six species of woodpeckers; interestingly, toucans and woodpeckers belong to the same order, Piciformes. However, his descriptions of play in woodpeckers do not resemble any recorded for toucans. Since much of the play behavior includes billing, which Armstrong (1965) interpreted as a ritualization of aggression, it seems likely that most of the play behavior in Red-billed Toucans is modified aggression that functions to maintain group cohesion.

Nestling Period

The nestling period in the Red-billed Toucan is very long. According to Skutch (1967a), cavity nesting birds tend to have longer nestling periods than birds of the same size with open nests. Nice (1957) documented higher breeding success for cavity-nesters as compared with open-nesters. I suspect that breeding success is low for Red-billed Toucans, because only one of five nests I observed fledged young. However, I have no way of assessing what effect, if any, my presence in the nest vicinity might have had in attracting predators.

When we compare the nestling period of this toucan with other neotropical cavity-nesters, we find that small trogons fledge at about 17 days of age, larger trogons at about 26 days, motmots and some woodpeckers at about 30 days, and large kingfishers at about 37 days (Skutch, 1971). The longer nestling period of about 48 days for Red-billed Toucans may be attributed to their larger size and low protein intake. The bulk of the food fed to the nestlings is fruit, whereas nestlings of trogons and motmots are fed greater amounts of arthropods (pers. observ.). So it seems likely that differences in diet and size might explain the longer nestling periods of Red-billed Toucans.

Summary

A life history study of the Red-billed Toucan (*Ramphastos tucanus*) was conducted at intervals from 1964 to 1966 and during the summer of 1971 at Karrow, Akarakuru, Atkinson Field, and Kibilibiri in Guyana.

This species inhabits forests of South America from the northern Amazon River basin to the Atlantic coast and west to the eastern Andes in Colombia.

The plumage of the Red-billed Toucan is alike in both sexes but males tend to be larger than females. Juveniles have duller plumage but are similar in body size to adults.

Toucans live in year-round flocks of from two to ten birds with approximately equal sex ratios and strong social bonds between mated pairs. There is a high incidence of courtship feeding throughout the year. Periodic bouts of play behavior occur and include bill-fencing, bill-pushing, fruit-passing, and tagging. Toucans roost in close contact with each other in the foliage of the canopy.

Red-billed Toucans never fly in uniform flocks but stagger their movements in swift and undulating flight. However, these toucans are weak long-distance fliers.

The Red-billed Toucan augments its frugivorous diet with cicadas,

caterpillars, lizards, and birds' eggs. Food is seized in the bill tip and is thrown into the throat by a backward toss of the head. Some food is held underfoot and torn apart.

The toucan's song is a loud, puppy-like yelp repeated several times while the head is tossed laterally and up and down, and the tail is jerked up and down. Its repertoire is limited to three notes—*yook*, *yeock*, and *yee-ock*. These same notes are used in protest calling. This species also produces a vocal castanet-like rattle during courtship feeding, nesting, intra- and inter-specific agonistic encounters, and in captivity.

The Red-billed Toucan nests from March to July. Mating takes place as early as December; conspicuous courtship was not observed. All nests were in natural cavities of living trees. A clutch consisted of two or three pinkish-white egs.

Both sexes incubated although the male apparently sat all night. The incubation period was 15.5 days ± 6.75 hours. The adults removed the eggshells from the cavity sometime after the young hatched.

The nestlings developed very slowly; eyes did not open until the third week and pinfeathers did not appear until the fourth week, at which time the nestling showed fear reactions. By the fifth week, they were fully feathered and exhibited exploratory behavior. A week later they were taking food at the cavity entrance. The fledglings left the nest between the 45th and the 49th day, at which time they were about the size of their parents but with duller bills and plumage.

Both parents brooded the nestlings quite often for the first two weeks. After 10 days of age, the only diurnal brooding occurred when it rained. The male did most of the night brooding but I recorded three night sessions for the female.

Both sexes fed the nestlings. Food was usually transported in the bill tip. Most of this food consisted of fruit, but cicadas, caterpillars, a locust, and a lizard were also recorded. The nestlings were fed at the cavity entrance from the 39th day until they fledged. Nestling fecal sacs were removed by the adults.

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BIRD DIVERSITY AND ABUNDANCE IN AMAZON FOREST COMMUNITIES

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The avifauna of the municipality of Belém in the Lower Amazon comprises between 450 and 500 species (Fernando Novaes and Paul Slud, pers. commun.). Approximately 300 of these have been recorded from the forest reserves of the Guamá Ecological Research Area. Of these 300 species, over 200 were captured and banded in a program initiated in the reserves in January 1963. Since that date, birds have been caught in nets approximately 20,000 times in study areas designed to sample the various forest environments.

The capture program was begun to collect data that would hopefully shed light on the epidemiology of various arthropod-borne viruses known to occur in the Belém region and was subsequently expanded to include more forest types, higher levels of the forest, and additional aspects of the ecology and biology of the birds. This was the first study in which a large number of individual birds was examined in a neotropical rain forest in a long and intensive capturing program.

The abundance of organisms and the diversity of communities have received considerable attention (MacArthur, 1957; MacArthur and MacArthur, 1961), especially in regard to tropical rain forests where species richness for birds reaches greatest values. One of the early papers on this subject (MacArthur, *et al.*, 1966) was the original inspiration for this study. MacArthur *et al.* suggested that birds recognized four layers of vegetation in rain forests as opposed to three in temperate forests. The field program at Belém was originally intended to measure the layers of birds, and the capture data will be analyzed eventually for this purpose. The basic data, however, were even better suited for investigating other questions about diversity and abundance for the first time with a large sample — questions concerning the level of diversity in these communities, the distribution of abundance, and the proportion of very rare species in the sample.

The forest environments where the birds were studied contain between 400 and 500 species of trees that are 10 centimeters in diameter at breast height (d. b. h.) and larger. These are distributed with respect to various environmental gradients in three main types of forest: dry ground (terra firme) forest, varzea (riverine) swamp forest, and permanent (igapó) swamp forest. All three forest types are included in the four study areas: Station A, Mocambo, Varzea, and Catú areas. The availability of tree data for the various study areas in conjunction with the large quantity of bird data makes it possible to examine certain questions about tropical rain forests for the first time. What are the inter-habitat abundance patterns of trees and birds? How do they differ? Why?

Methods

Location

Belém, the capital city of Pará state in Brazil, lies at 1° 26′ S Lat., within 150 kilometers of the equator and of the Atlantic Ocean. On the outskirts of the city and bordering the Guamá River lies the Instituto de Pesquisas e Experimentacão Agropecuarias do Norte (I.P.E.A.N.) of the Brazilian Ministry of Agriculture. Part of its forested lands have been set aside as a study reserve, the Guamá Ecological Research Area (Área de Pesquisas Ecológicas do Guamá = A.P.E.G., Figure 1). The rainfall is somewhat over 2,800 millimeters per year (Table 1). The mean temperature varies only one degree from month to month, from 25° to 26° C. All the study areas lie less than 20 meters above sea level. The forests of this region are classified as tropical rain forest by Richards (1952). All forest types studied appear to be affected by rather brief, localized, but sometimes exceedingly violent, storms.

The Study Areas

Figure 2 represents an idealized transect from the Guamá River inland. Along the river's edge lies a swamp forest known as varzea forest. This swamp forest is subjected to flooding twice daily due to tidally induced fluctuations in river level. In addition, the river rises and falls annually due to seasonality in rainfall. Near the river's edge, a natural levee built from silt deposited by the flood waters is interrupted at intervals where streams dissect the swamp forest. This is known as high varzea or varzea alta. The lower parts of the swamp farther away from the river's edge are known as varzea baixa, or low varzea, and have a large number of palm trees of various species.

Farther inland, as the land begins to rise, a transition occurs from varzea forest to high ground, or terra firme, forest. The soil changes from a clay to a laterosol. Terra firme forest has a more closed canopy and fewer palms; it is rich in tree species. In the Mocambo forest, 295 species with d.b.h. of 10 cm or larger have been identified in an area of 5.5 hectares (Hatheway, 1971). This forest is essentially undisturbed, whereas at Station A even the tallest terra firme has been somewhat disturbed and is not as tall as the Mocambo forest.

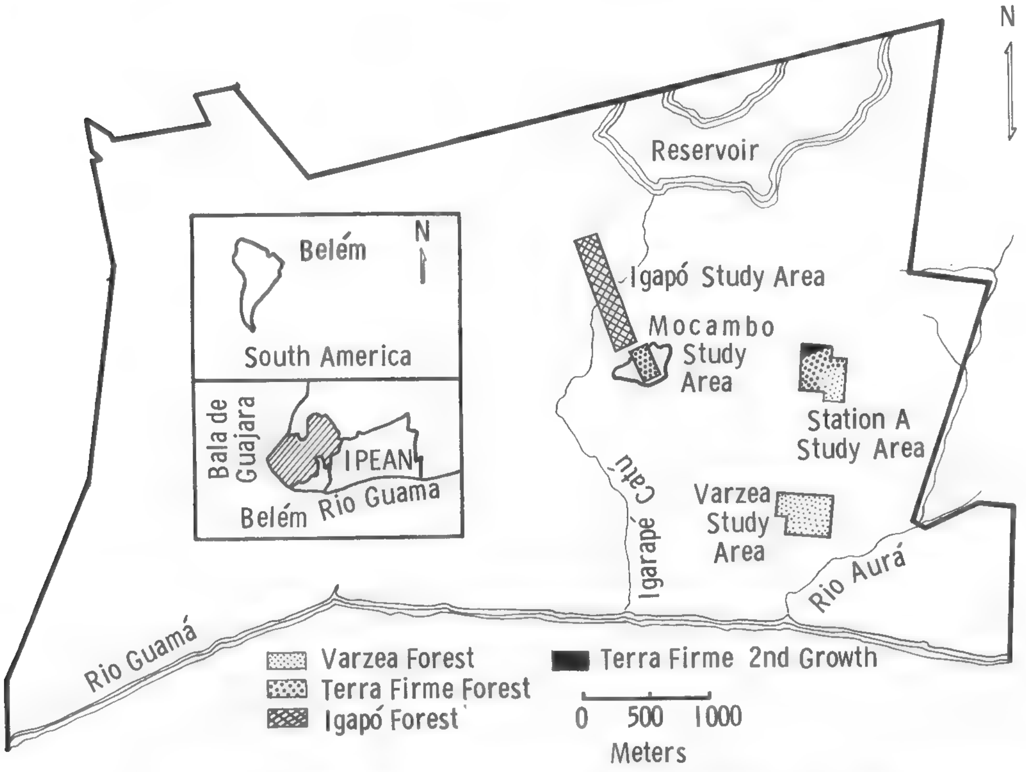

Figure 1. Location of study areas near Belém in the Lower Amazon. Areas included various forest types and were located on the grounds of the Instituto de Pesquisas e Experimentacão Agropeduarias de Norte.

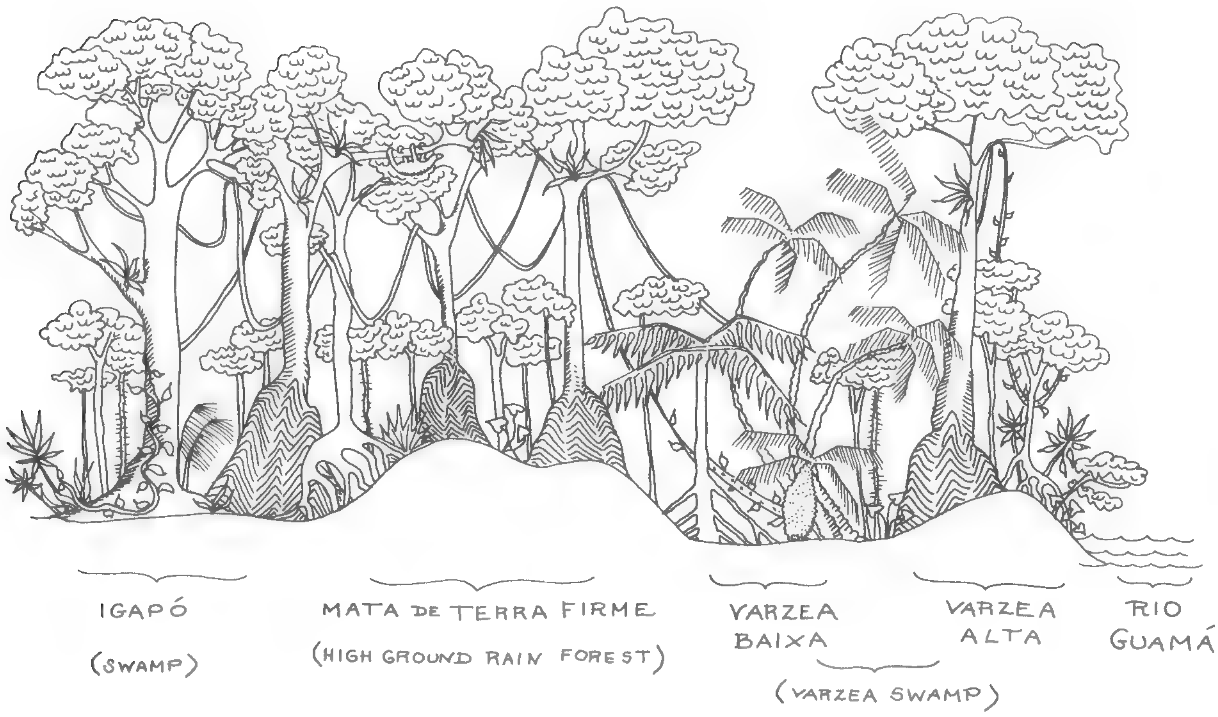

Figure 2. A hypothetical transect from the Guamá River inland.

In low-lying areas not at the river's edge occurs a permanent swamp forest, the igapó swamp forest. This is continuously flooded with blackish water, more so in the rainy season. It is a somewhat more open forest than the varzea or terra firme.

Four bird capture study areas (Figure 1) were chosen to sample all the forest types of the APEG reserves. The Station A study area includes terra firme (high ground) forest, second growth (capoeira), transition between terra firme and varzea swamp forest, and varzea itself. The Mocambo study area is on an island of terra firme forest basically undisturbed by man (Cain, *et. al.*, 1956) and has most recently been described by Hatheway (1971) and Elton (1973). The Varzea study area is in the middle of the partly disturbed varzea swamp in the main APEG reserve about one km south of the Guamá River. The Mocambo island is largely bounded by igapó swamp forest wherein lies the Catú, or Igapó, study area. In the swampy areas, boardwalks were built to facilitate movement. All the study areas fit in a circle two km in radius.

Deployment of Nets

In each of the study areas I used mist nets to capture birds. Some of the nets were suspended between poles to capture birds flying between 15 cm and two meters above ground level. I raised other mist nets, usually in sets of three, but occasionally in sets of two or four, by means of a rigging of nylon line to various heights above the forest floor (Humphrey, *et. al.*, 1968). The highest of these was 23 meters above the forest floor at the net's highest point.

For some analyses, data from groups of three nets were lumped. The criteria for these net groups were: a) that the three nets be adjacent, and b) that all three be from similar forest type. Only low nets are considered in the following descriptions of the study areas. High nets generally lay within the area enclosed by low nets, or very close by. Table 2 lists the number of nets represented by low and high nets and also net-groups for all areas and habitats.

The Station A study area consisted of two parts, "Old Station A" and "New Station A." Captures took place at least once a week between 5 October 1967 and 14 August 1969 with only a very few exceptions. Eighty-seven to eighty-nine low nets originally used in this study area were augmented by five more when boardwalks went into operation beginning in June 1968. Due to the criteria used in determining net groups, I used only data associated with 87 nets in some analyses.

The New Station A area was first in operation on 4 June 1968 and, beginning 9 July 1968, was used for captures according to the capture cycle described below until the final capture on 14 August 1969. Station A had 15 six-meter-high and 52 12-meter-high nets on a total of 22 high net rigs.

The Mocambo study area was the smallest and least used area. We located the low nets around the borders of two adjacent hectares and first used them on 6 November 1967. A portion of the nets were open on 16 April 1968 and, beginning with the capture of 13 August 1968, we operated the area on the standard cycle until the last capture on 7 August 1969. This area contained no high nets.

The Varzea study area comprised 45 low nets first used on 30 April 1968 and operated on a regular cycle from 16 July 1968 through 21 August 1969.

The Catú, or Igapó, study area included 40 low nets strung along a transect one km in length through the swamp forest. We first used these nets on 15 April 1968 and operated them on a regular basis beginning 2 July 1968 through 7 August 1969.

Bird Capture Data and Field Procedure

I collected most of the data in three-week cycles: Week 1, captures on Tuesday and Thursday at the Varzea area and a half-day capture on Friday at Old Station A; week 2, captures on Tuesday and Thursday at the Catú and Mocambo areas and a half-day capture at Old Station A on Friday; week 3, captures on Tuesday at New Station A and one half of Old Station A, and Thursday at New Station A and the other half of Old Station A. Consequently, for each capture-area except Old Station A, the birds were not subject to netting for 18 days after two captures a day apart. We maintained this schedule to minimize both the development of net shyness in the bird populations and the complex record keeping necessary when bleeding individual birds.

On full capture-days, we began opening the nets at approximately 05:30 hours and began closing them at 16:30. On half days closing began at 10:30. Field assistants opened specific sets of the numbered nets, keeping track of the times of opening and closing in a notebook. Thereafter, we visited the nets as frequently as every 45 minutes when possible.

Whenever a bird was taken from the net, we recorded the date, time, species, net number, and band number, if the bird was a recapture. If the bird had already been captured that day, we released it immediately. Otherwise, we brought the birds to a small cabin to be processed by a team of three persons and banded if necessary. We processed birds in a sequence that provided the weaker species with the shortest waiting period before examination. Hummingbirds, for example, were processed right away; this practice, combined with feeding sugar water to weak individuals, eliminated a large mortality problem with this particular family. We recorded data in complicated redundant fashion to reduce error and omission.

Vegetation Data

As part of an overall inventory study of the APEG reserves in certain areas, trees with d.b.h. greater than 10 cm were numbered, identified, measured, and recorded under the supervision of J. Murça Pires, IPEAN botanist. This inventory was not completed, so full data were available only for the Mocambo study area. Tree identifications and d.b.h. were available for about half of the Catú area and for three hectares of Station A.

Early in 1970, thanks to J. M. Pires, woodsmen of the Seçao de Bôtanica of IPEAN identified and recorded trees in the Varzea and Station A netting areas. They censused trees in 10-meter plots so as to obtain a sample of trees within 10 meters of each mist net, obtaining data from six quadrats for each mist net, representing a 20 × 30 meter rectangle with the net essentially in the center. Not all nets had the full complement of six quadrats of tree data.

Preparation of Data for Electronic Data Processing

We prepared only bird capture data from October 1967 through August 1969 for analysis, because all forest types were not included prior to this time. This reduced the number of captures of birds for analysis to approximately 15,000.

Both the tree and bird data were transferred to IBM punch cards for electronic data processing. The tree data, including quadrat number, species, number of the net within 10 meters, and d. b. h., where available, were punched from the original field data sheets. The cards were not verified, because of expense and time, but they were inspected visually. A certain residual amount of error in punching undoubtedly exists in the data.

TABLE 1

Rainfall (mm) at the IPEAN and IPEG Weather Stations

Month	*IPEAN*		*APEG*		
	1923-1963[1]	1966	1967	1968	1969
Wet season:					
January	335	371 (28)[2]	428 (26)	224 (21)	404 (22)
February	423	482 (26)	352 (27)	224 (20)	384 (25)
March	455	472 (28)	495 (28)	339 (26)	322 (25)
April	379	456 (25)	438 (22)	382 (21)	454 (26)
May	279	411 (25)	343 (24)	355 (29)	372 (26)
June	169	291 (19)	163 (15)	104 (19)	117 (13)
Total	2,040	2,483 (151)	2,219 (142)	1,628 (136)	2,053 (137)
Dry season:					
July	150	179 (18)	96 (12)	59 (10)	167 (19)
August	117	164 (14)	137 (17)	144 (12)	126 (15)
September	124	143 (18)	113 (13)	113 (16)	152 (21)
October	106	81 (12)	54 (7)	165 (13)	31 (11)
November	94	175 (12)	37 (3)	268 (22)	70 (10)
December	206	181 (17)	110 (14)	158 (18)	70 (13)
Total	797	923 (91)	547 (66)	907 (91)	616 (89)
Year Total	2,837	3,406 (242)	2,766 (208)	2,535 (227)	2,669 (226)
		Mean APEG yearly rainfall: 2,844 mm			

[1] Average for a 41-year period.

[2] Figure in parentheses indicates number of days with rain.

The original bird field slips were a mixture of Portuguese, English, Latin, and numbers. Thus, the bird data had to be coded onto coding sheets before key punch operators could transfer them to IBM cards. There is one IBM card for each field slip (and capture number), and each one includes date, location, species, band number, net and shelf number, and other data not used in the present analyses. These cards were not verified but a number of programs were run to pick out unreasonable numbers, such as capture times after 18:00 hours. A more complex program checked data associated with band numbers to pick out such errors as a band number having different species numbers associated with it on different occasions.

After corrections were made, final magnetic tapes were prepared from the tree cards and bird cards.

Biases in the Bird Capture Data[1]

(1) Species differ in habits, such as flight pattern. Consequently, some species are more likely than others to be caught in mist nets. This may make it unlikely that a particular species will be caught in a mist net. For example, the various species of tinamous are more readily captured in

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[1] In a posthumous paper (MacArthur, R. H., and A. T. MacArthur, 1974, The use of mist nets for population studies of birds, Proc. Nat. Acad. Sci., 71:3230–3233), Robert MacArthur presents a discussion of biases in mist netting data from a different point of view.

rodent live-traps than mist nets, probably because they just walk under the nets. Were it not for the frequent distinct calls of the various species of tinamous, there would be no indication of their prevalence in the Belém forests. Such birds represent an extreme form of net avoidance. Fortunately, most birds do not present such problems and, as a result of the large numbers of nets and the long period during which they were used, it is likely that the majority of birds living in each of the study areas was captured during the course of the study.

(2) Another sort of bias is encountered if calculations dealing with individuals assume the birds are alive and present for the entire duration of the study. Then, birds that fledged or died within the time of the study are counted as if they lived longer than they did. In terms of adult birds, the distortion from this assumption perhaps is not very great, in part because the adult mortality rates of tropical forest birds are only on the order of 10 to 15 percent per year (Snow, 1962a, 1962b; Fogden, 1972). Bias also exists if calculations assume that mortality rates are similar among all bird species in the Belém forests, so that any distortion of the number of individuals from this source is similar for all species and cancels out when calculating such things as diversity and relative abundance. This, of course, is not entirely true, since larger species presumably have lower death rates than smaller ones. One could partly correct for this particular bias by computing relative biomass or relative existence energy as Karr (1968, 1971) has done for Panamá and Illinois birds.

(3) Greater distortion of the data probably arises from differences in juvenile mortality between species, but since we cannot distinguish juveniles from adults in all species, it is not possible to analyze adults alone. When this does become feasible, it will be possible to get figures more

TABLE 2

The Number of Mist-nets in the Study Areas[1]

	High net rigs	*Nets on high net rigs*	*low nets*[2]	*Nets in net groups*
Station A				
Second growth	—	—	26, 0	24
Terra firme	6	10 (+9)	27, 6	27
Terra firme—varzea transition	4	9 (+3)	46,12	45
Varzea	12	33 (+3)	38,27	33
Mocambo	—	—	32 (+12)	30 (+5)
Varzea				
Complete	20	51 (+12)	45	33
Depressions	8	21 (+3)	21	15
High ground	13	30 (+9)	24	18
Igapó	20	43 (+15)	40	36

[1] Numbers in parentheses are 6-meter nets; all others are 12-meter nets.

[2] Second number is the number of nets in New Station A only.

comparable to ones derived from breeding bird censuses in the temperate zone.

(4) Bias may also exist if a bird caught only once during the 23 months received a weighting in calculations equal to a bird caught several times. The bird caught only a single time may be a transient individual, one with a home range just touching the study area, a juvenile dispersing from the area, or a bird from a higher stratum of the forest. Until we have a better understanding of the biology of the various species, estimates of territory size in particular, we cannot correct for some of these sources of error. In this study, for example, ant-following species are represented by more individuals because they are attracted from a much larger area than most other birds. This is a consequence of the nomadic nature of their food supply and the adaptation of their territorial system to cope with it (Willis, 1967). In other areas, such as Perú (Terborgh and Weske, 1969) and Panamá (Karr, 1971), species of relatively nomadic manakins (genus *Pipra*) show figures of relative abundance that represent a larger proportion of the bird population (ca. ⅓) than is correct. This probably is less true in Belém where no manakin is the most abundant species in any of the forests studied.

(5) Because of the small size of the feet of hummingbirds and the absence of special bands for them, we used a simple marking system based on clipping wing and tail feathers. Such markings were erased by molting. Unless we recaptured an individual before it had replaced the clipped feathers, we could not determine whether an unmarked bird was one that had been captured and marked before moulting. Consequently, the numbers of hummingbirds recorded might approach twice as many as the number we really handled.

(6) Our netting data do not fully represent canopy species; only nets elevated above the canopy might adequately sample these species. Observations on the canopy avifauna from a 35-meter tower provide a basis for estimating the bias introduced by this factor.

(7) Another bias arises from the assumption that, for a given net or net group, nothing other than the environment in which it is placed affects the likelihood of catching a particular species or birds in general. This is not totally realistic because a net placed across a trail, for example, may be more likely to catch a bird or a particular species than one placed along a trail. The large number of nets in each forest type compensated somewhat for this and similar problems.

(8) Net shyness — the tendency to avoid a net after being captured in it — develops more readily in some species than others and in individuals occurring closer to nets. We designed the netting cycle to minimize the development of net shyness, but the premise that a bird will not remember being caught in a particular location after an 18-day interval is incorrect. Capture rate measured in birds per net day or net hour fell slowly over the course of the study. The capture rate for each Tuesday in a given area was almost always higher than the rate of capture two days later. Net shyness probably explains why the Scale-backed Antbird (*Hylophylax poecilonota*) was caught in numbers during the first Mocambo capture and almost never thereafter. Figure 3 represents the presumed effect of net shyness on the frequency of capture (vertical axis) of an individual bird. The effect could not have been terribly great. Otherwise, capture rates would have fallen swiftly to very low levels.

(9) Net avoidance — the tendency for a species to avoid actively nets without any prior contact with a net — is only characteristic of some species and is a consequence of the biology of the particular species. It might, for example, represent a strong response to human activity in the study area. Net avoidance is essentially a special case of item 1: particular habits that render the capture of a particular bird unlikely.

Usually, however, net avoidance probably has an effect similar to that represented by Figure 3. If the upper curve represents the normal frequency along one dimension of the environment of a single bird, net avoidance probably will result in mist net data similar to the lower curve. In other words, a bird will avoid nets to a similar degree along the gradient resulting in a lower, narrower curve that does not change in shape. The extent of this effect, measurable by B, cannot be measured with the data. Net avoidance and net shyness can, of course, occur in the same species.

(10) After examining the birds, we released them, almost always from the cabin in the study area in which they were caught. Occasionally, we caught individuals again before the end of the day. I included these same-day recaptures in the frequency calculations; but the number of such captures was never as great as 10 percent of the total captures on a single day, and frequently was less.

For calculations based on individuals, I eliminated same-day recaptures except when fewer than all the nets in an area were included in the calculations. Unfortunately, the computer programs were designed so that they could not recognize an individual as a same-day recapture unless it first was caught in one of the nets under consideration. This means that calculations sometimes will include a bird atypical of a forest type simply because the bird had to pass through it to return to its normal forest type.

This latter problem is of no consequence execpt at Station A. The Mocambo cabin was located in an ecotone between the igapó and terra firme and there were no low nets within 20 meters of the cabin. In the Varzea area, the cabin was in varzea forest. At Station A, however, the cabin was in terra firme forest and birds caught in the varzea portion of that area had to pass through terra firme and terra firme-varzea transition on their return flight. Similarly, birds caught in terra firme-varzea transition had to pass through terra firme. So did birds caught in second growth (capoeira) but the distance was very short in this case.

Other ways in which mist netting affects the ecology of birds under study have recently been discussed by Nisbet and Medway (1972).

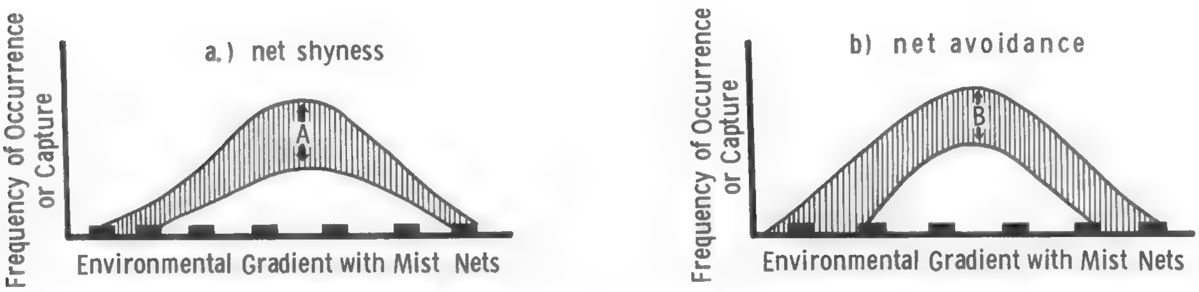
Frequency of Occurrence or Capture
a.) net shyness
A
Environmental Gradient with Mist Nets
Frequency of Occurrence or Capture
b) net avoidance
B
Environmental Gradient with Mist Nets

Figure 3. Net shyness (requiring contact with nets to develop) and net avoidance (no net contact required) affect capture data. The upper curves represent real frequency of a bird along the environmental gradient being sampled. The lower curves represent actual netting data.

DIVERSITY [1]

The Belém avifauna is rich in the number of species and the available samples from this study were much larger than any ever analyzed for tropical rain forest birds. In investigating this diversity, I took into account two components: (1) the number of species, and (2) the evenness of distribution of abundance among the species. Heretofore, ample data on relative abundance have not been available for tropical rain forest bird communities (Tramer, 1974).

The Belém forest avifauna is probably one of the most species-rich in the world. Most of the species recorded from the municipality of Belém inhabit forests, very few water birds and relatively few birds found exclusively in open country being present. Only one forest bird migrates. Some of the large birds, such as the guans and curassows (family Cracidae) and macaws (family Psittacidae) are no longer present in Belém forests, but their absence has little effect on the total number of species. It is unlikely that any environment similarly lacking in altitudinal variation has a richer avifauna with the possible exception of western Amazonia. Certainly, the African lowland rain forests are species-poor in comparison with the Belém forests (Moreau, 1966).

Appendix 1 describes the methods used for calculating diversity.

Results

The figures for species diversity (H′ base 2) for all the capture data and mean values and standard deviations are shown in Tables 3 to 6. The diversity index (H′, base 2) ranges from 5.05 to 5.82. For the first 100 birds caught (Table 7), the diversity index values are lower than values for all data, and range from 3.44 to 4.91 for Belém and from 4.11 to 4.44 for the Peruvian data.

The preponderance of rarity is shown in Tables 8 and 9. The evenness of abundance distributions (J and J′) are shown in Tables 10 and 11 and Figures 5 and 6. The regression line of H′ against H_{max} for the Belém capture data is described by the equation

$$H' = 0.479\,(H_{max}) + 2.322$$

and is shown graphically in Figure 9. The data used were the values in Tables 3 to 6. Additional data were used in calculating this regression, namely data from net groups, and are a subset of the low net data. Their main effect is to dampen the effect of the high H′-low equitability points in the regression and their omission would merely strengthen the conclusion. The fit of the data to the linear form is good ($r = 0.854$) and the F test provided a probability value of greater than 0.995. The results show no great variation in patterns of relative abundance.

Vertical stratification figures are shown in Table 13, while Table 14 records of the horizontal component diversity for Belém and the North American forests. We caught 53 of 186 species in only one Belém forest type. Figure 7 shows the number of breeding species plotted against area.

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[1] A recent discussion of diversity (Peat, R. K., 1974, The measurement of species diversity, Ann. Rev. Ecol. and Syst., 5:285–307) appeared subsequent to submission of this manuscript.

The Lower Amazon curve is higher than that for Vermont, but is of similar slope. Ohio points are essentially the same as those for the Vermont curve.

Discussion

H versus H′

The use of H′ as a diversity index assumes that the data represent an unbiased sample from an infinite population. This is the same as assuming that there are no species lacking in the sample, and that the relative abundances of the species are the same as in the population which has been sampled.

These are probably reasonable assumptions when dealing with a sample of *Daphnia* from a lake, but as Pielou (1966, 1969) pointed out, they are not reasonable when dealing with data such as a census of breeding birds in a forest or data such as those from the Belém forests. In such a case, H is appropriate as it measures the "information content" or diversity of a complete enumeration without reference to the population being sampled.

Tables 3 through 6 show that in the case of the Belém data, results for H and H′ (using logarithm base 2) are much the same. In all cases, H is somewhat less than H′, which can be shown mathematically to be always

TABLE 3

Diversity of Belém Forest Bird Communities
(Calculated from all birds caught in all nets)[1]

	N[2]	*S*	*H*	*H′*[3]	*H′ (base 2)*[4]	H_{max}	$1/\Sigma(p_i)^2$
Station A							
All habitats	3,078	161	5.69	4.04	5.82	7.34	33.59
Terra firme	735	104	5.44	3.99	5.76	6.70	34.19
Terra firme—varzea transition	1,206	110	5.41	3.90	5.62	6.79	30.42
Varzea	1,044	106	5.22	3.78	5.45	6.73	24.75
Varzea	1,767	125	5.43	3.88	5.60	6.98	26.65
Igapó	1,782	127	5.58	3.99	5.76	6.99	30.30

[1] Station A capoeira and Mocambo are not included as they had only low nets.

[2] Letter headings indicate the following:
N = number of individuals
S = number of species
H and H′ are diversity indexes using natural log base (e)
H′ base 2 is the diversity index using a log base of 2
H_{max} is the maximum diversity with S species and equals $\log_2$ (S)
$1/\Sigma (p_i)^2$ is another diversity index

[3] $\overline{H'} = 3.93 \pm 0.09$

[4] $\overline{H'} = 5.67 \pm 0.13$

true (Pielou, pers. commun.), but the discrepancy is not great. So, although it is not mathematically rigorous to use H′ in place of H, in this case where tremendous precision is unnecessary, H′ is satisfactory for use. Whittaker (1972) cites other reasons to prefer H′ to H.

Effects of Biases in the Data

Most of the various biases in the data, described above, will not have much effect on measurements of diversity. This is because so many different nets make it improbable that a particular bird would manage to avoid them all for the entire period of the study. We still caught new individuals toward the end of the study; and because of the effects of net shyness, these represented one-fifth to one-quarter of a day's capture by that time. Most of these, however, were probably young birds.

Two biases that probably reduce the diversity values below reality are the ones resulting from net avoidance and from behavioral differences, rendering some species less likely to be caught than others. The under-representation of canopy birds also reduces the values, probably more from an under-representation of relative abundance than of species.

In contrast, the overestimation of the number of hummingbirds may have increased the diversity values. Certainly, if we exclude hummingbirds from the calculations, as in Tables 4 and 6, the diversity values almost invariably decrease. This partly reflects the generally high abundance of hummingbirds. If one estimates that hummingbird numbers are about one

TABLE 4

Diversity of Belém Forest Communities

(Calculated from all birds except hummingbirds caught in all nets)[1]

	N[2]	*S*	*H*	*H′*[3]	*H′ (base 2)*[4]	H_{max}	$1/\Sigma(p_i)^2$
Station A							
All habitats	2,414	149	5.56	3.96	5.72	7.23	29.25
Terra firme	622	94	5.22	3.84	5.55	6.55	27.96
Terra firme—varzea transition	1,051	100	5.23	3.78	5.46	6.66	25.96
Varzea	704	96	5.21	3.81	5.50	6.58	26.69
Varzea	1,265	114	5.50	3.96	5.71	6.83	33.38
Igapó	1,280	117	5.58	4.02	5.80	6.87	35.63

[1] Station A capoeira and Mocambo are not included as they had only low nets.

[2] Letter headings indicate the following:
N = number of individuals
S = number of species
H and H′ are diversity indexes using natural log base (e)
H′ base 2 is the diversity index using a log base of 2
H_{max} is the maximum diversity with S species and equals $\log_2$ (S)
$1/\Sigma(p_i)^2$ is another diversity index

[3] $\overline{H'} = 3.90 \pm 0.09$

[4] $\overline{H'} = 5.62 \pm 0.13$

and one-half times their real values, then it is not unreasonable to consider that the overestimation of hummingbird numbers largely compensates for the other biases that tend to depress the diversity figures.

Level of Diversity of the Belém Forest Avifauna

The diversity figures for the birds of the Belém forests (Tables 3 to 6) are higher than any published for any other animal or plant communities. The high values reflect not only the high diversity, but also the appropriately large sample size. Almost all diversity figures for birds in the literature are H′ with base 2 or base e, so there is little with which to compare our calculations of H and $1/\Sigma(p_i)^2$.

Almost all published values of diversity (H′) for neotropical forests have used the natural logarithm base e. Figures for H′ (base e) for Belém and based on all birds caught range from 3.78 to 3.99 with a mean value of 3.93 ±0.09 (Table 3). H′ was also calculated for the data from all the forest types at Station A lumped together and is only slightly higher. If hummingbirds are eliminated from the calculations, values for the various forests range from 3.78 to 4.02 with a mean value of 3.90 ±0.09 (Table 4).

Orians' (1969) estimates of diversity (converted to base e from base 10) for a number of Costa Rican forests range from 2.88 to 3.80. Censuses from Panamá by MacArthur *et al.* (1966) yielded values of 3.39 for the forest on Barro Colorado Island and 3.38 for young forest on the Chiva Chiva Road. Karr's (1971) figures for some Panamá censuses are closer to Belém values, being 3.46 for early shrub, 3.73 for late shrub, and 3.65 for moist forest. Karr's study areas would probably be closer to the Belém figures were it not for the abundance of a single species, the Red-capped Manakin (*Pipra mentalis*), which accounted for roughly 30 percent of his sample.

For one of the censuses included by Tramer (1969), one he made on Barro Colorado in January of 1969, he gave a diversity value (H′, base 2) of 4.38. H′ (logarithm base 2) calculations for two Mexican censuses, a tropical rain forest in Veracruz (Davis, 1955) and a lowland tropical forest in Veracruz (Davis and Moroney, 1953) resulted in diversity indexes of 5.31 and 5.55, respectively. For these calculations, only those species were included for which numerical values of abundance were provided. Had those marked only as "present" been included, values would have been higher. In any event, those values are similar to, but lower than, those for Belém. The diversity index (H′, base 2) for Belém ranges from 5.45 to 5.76 for all birds, with a mean value of 5.67, and from 5.46 to 5.80 (mean = 5.62), if hummingbirds are excluded. Although we calculated the species diversity for all Station A habitats lumped together for the sake of completeness, I did not include those values in the discussion.

If data are restricted to low nets, the values of species diversity (H′, Tables 5 and 6) fall somewhat, reflecting the exclusion of diversity due to vertical stratification of the avifauna and perhaps the reduced sample size, as well. Two areas, the Station A second growth, or capoeira, and Morcambo had only low nets. Here, and in the calculations based on net groups, the diversity index (H′, base 2) for all birds ranges from 5.24 to 5.58 with a mean value of 5.43, and from 5.05 to 5.37 with a mean value of 5.25, if hummingbirds are excluded.

Plate I. Ringed Antpipit (*Corythopis torquata*). Painting by John P. O'Neill.

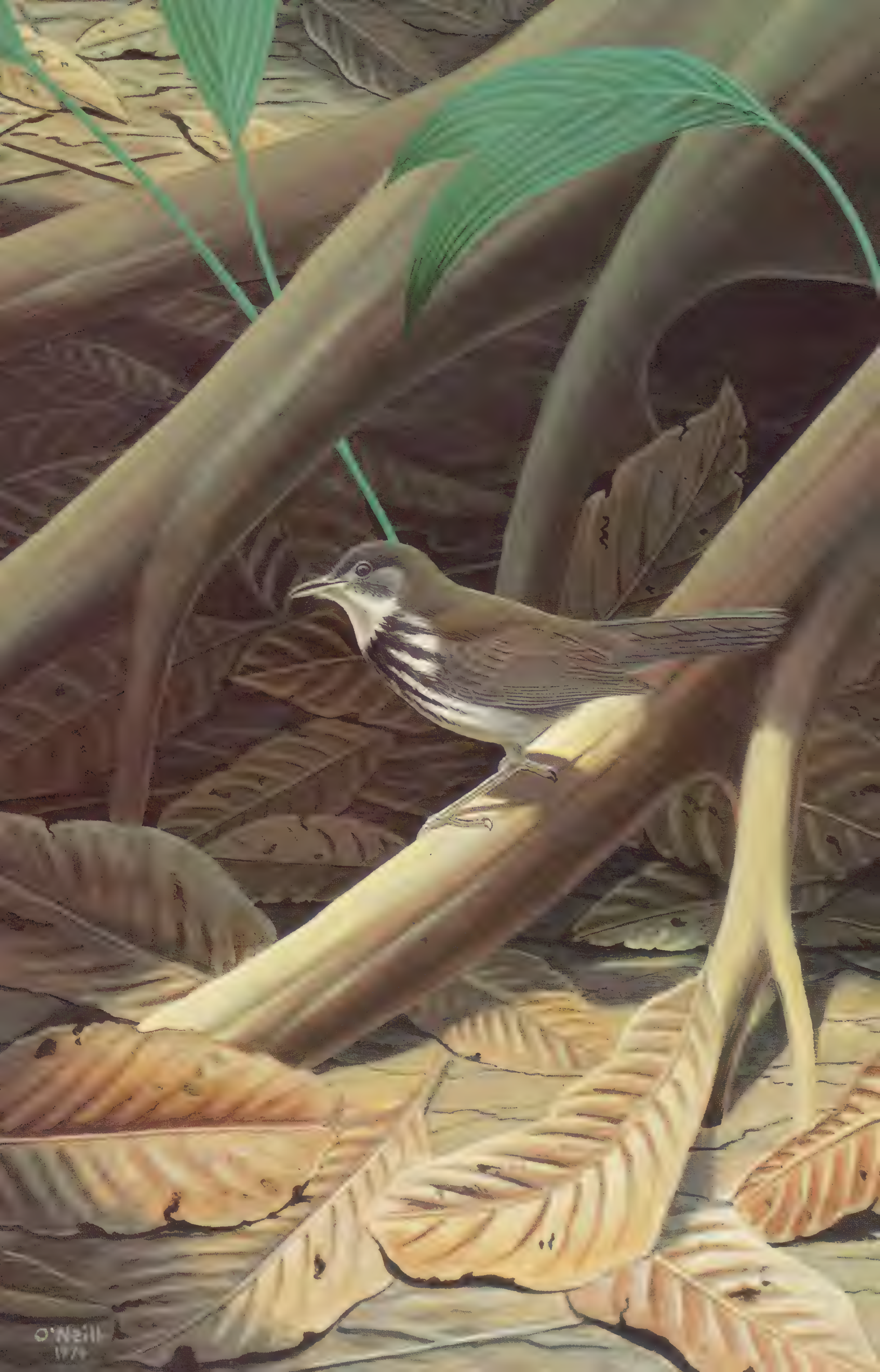

O'Neill
1974

TABLE 5

Diversity of Belém Forest Bird Communities
(Calculated from all birds caught in low nets)

	N^1	S	H	H'	H' (base 2)	H_{max}	$1/\Sigma(p_i)^2$
Station A							
All habitats	2,495	128	5.58	3.96	5.71	7.01	34.38
Capoeira	898	100	5.20	3.78	5.45	6.64	26.47
Terra firme	507	66	4.94	3.63	5.24	6.04	25.07
Terra firme—varzea transition	1,103	99	5.36	3.86	5.58	6.64	30.59
Varzea	684	77	5.15	3.75	5.41	6.27	29.56
Mocambo	474	75	5.09	3.77	5.44	6.23	27.08
Varzea	1,112	87	5.28	3.80	5.48	6.44	31.27
Igapó	1,088	93	5.19	3.74	5.39	6.54	28.28

[1] Letter headings indicate the following:
N = number of individuals
S = number of species
H and H′ are diversity indexes using natural log base (e)
H′ base 2 is the diversity index using a log base of 2
H_{max} is the maximum diversity with S species and equals $\log_2$ (S)
$1/\Sigma (p_i)^2$ is another diversity index

Ultimately, the high levels of diversity of bird communities in western Amazonia may be shown to exceed those of the Belém region. Unpublished data collected by Philip S. Humphrey, who used only low nets in Amazonian Ecuador (Santa Cecilia, on the rio Aguarico, Napo Province, 0° 3′ N Lat., 76° 58′ W Long., altitude 340 meters), yield a species diversity (H′, base 2) value of 5.75. Although the sample of 124 species (n = 1,203) represents frequency data and is not strictly comparable to standard census data, it suggests an even higher bird species diversity in western Amazonia. Initial reports from the Manu National Park in Amazonian Peru (Terborgh, pers. commun.) tend to confirm this. Likewise, Pearson (1975a) lists 182 and 152 species for rain forest censuses in Amazonian Ecuador and Amazonian Peru, respectively.

Diversity of First 100 Birds Caught

Three existing studies (Karr, 1971; Terborgh and Weske, 1969; Vuilleumier, 1972) recorded a rather inadequate estimate of diversity by calculating the diversity index (H′) for the first 100 birds caught in mist nets. This is a convenient calculation to make, because p_i is simply equal to the number of individuals divided by 100. Furthermore, if net sites have been set up with minimal disturbance, there should be little bias from net shyness, in contrast to a netting area that has been worked for some time.

It has two drawbacks, however. The first is the probability of getting a poor estimate of diversity due to the effects of random chance on a small sample. For example, the values of 2.76 and 2.80 (Table 7) for terra firme-varzea transition are quite low. This is because a flock of 27 Silver-beaked Tanagers (*Ramphocelus carbo*) were among the first 100 birds caught. If all individuals captured are considered, this species has a relative abundance of less than three percent. The Station A capoeira sample is another example and is discussed below.

The second drawback is that small sample size, itself, results in an underestimate of diversity. A positive correlation exists between increasing sample size and rising diversity values, as can be seen by comparing values for low nets and for net groups. This was just why Sanders (1968) proposed the rarefaction method which sometimes tends to overestimate species diversity (Fager, 1972; Simberloff, 1972).

Vuilleumier's (1972) anomalous results for Chile easily could have been attributed to these two drawbacks; later, Church (1974) showed there was miscalculation as well.

Data in Table 7 analyze the first 100 birds caught in low nets and all nets in the Belém region. Station A had actually been used for captures before this investigation, but not immediately prior to the study; capture rates were comparable to the other areas, which had never had any previous captures.

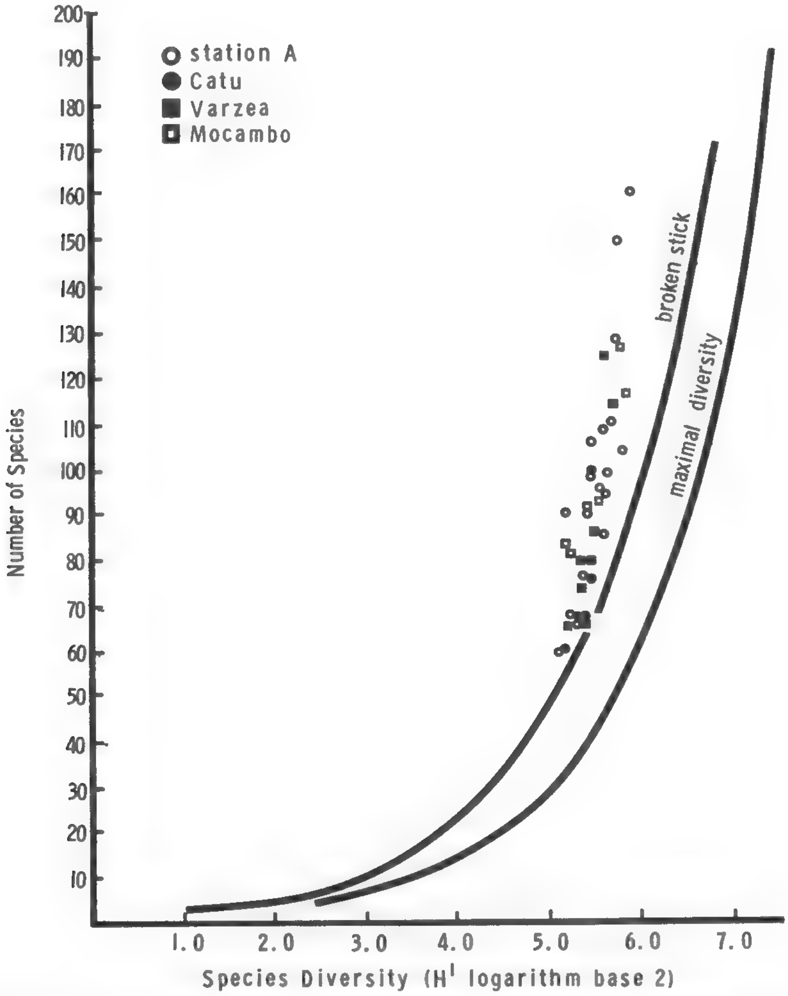


Figure 4. Points show how diversity of Belém forest bird communities, as measured by H' (log base 2), increases with species number. If abundance is continually readjusted with increasing species number to maintain equal abundance among all species, diversity would increase as in the "maximal diversity" line. If the distribution pattern followed the MacArthur "broken stick" model (Appendix 1), as species number increased diversity would follow the other line.

TABLE 6

Diversity of Belém Forest Bird Communities
(Calculated from all birds except hummingbirds caught in low nets)

	N[1]	*S*	*H*	*H'*	*H' (base 2)*	H_{max}	$1/\Sigma(p_i)^2$
Station A							
All habitats	2,109	118	5.40	3.84	5.55	6.89	29.25
Capoeira	800	91	4.99	3.63	5.24	6.51	22.42
Terra firme	463	59	4.76	3.50	5.05	5.88	21.99
Terra firme—varzea transition	978	90	5.18	3.74	5.40	6.51	26.26
Varzea	549	68	4.97	3.64	5.26	6.09	25.42
Mocambo	440	67	4.92	3.64	5.26	6.07	24.00
Varzea	918	80	5.15	3.72	5.37	6.32	28.56
Igapó	949	83	4.98	3.59	5.18	6.38	23.78

[1] Letter headings indicate the following:
N = number of individuals
S = number of species
H and H' are diversity indexes using natural log base (e)
H' base 2 is the diversity index using a log base of 2
H_{max} is the maximum diversity with S species and equals $\log_2$ (S)
$1/\Sigma(p_i)^2$ is another diversity index

There is little difference in all-net and low-net figures for Station A, because only one or two high nets were operational at the beginning of netting in each forest type. The Varzea and Igapó areas, however, were not used until all nets were functional. Values for all nets for the latter two areas are higher than for low nets, as anticipated on the basis of vertical stratification.

Values of species diversity (H', base 2) for low nets range from 3.70 for second growth (capoeira) at Station A to 4.80 for the Mocambo (terra firme). Comparable figures from the Amazon lowlands of Perú (Terborgh and Weske, 1969) are also presented in Table 9. The values for the cacao and coffee plantations and the matorral (a river's-edge forest) are not of too much relevance to this study except that they are generally of the same order of magnitude. The plantations had an overstory for shade — either planted or the remnant of original forest. It is of interest that, although the foliage profiles differed, the value of species diversity (H') for birds did not. The values for forest in 1965 and 1966 are most comparable to the Mocambo value; that they are lower is not surprising because of the abundance of the Band-tailed Manakin *(Pipra fasciicauda)* and because of the difficulties in identifying the small birds of the higher vegetation strata. The Station A terra firme value is closer to those of the Peruvian forest, but this is an artifact of the disturbance of that Belém forest.

I recorded a considerably lower value for second growth (capoeira) in Belém than for Perú because of a sampling artifact. When the first 100 birds were being caught, White-bearded Manakins (*Manacus manacus*) were at the height of their annual display cycle. Also, a swarm of army ants

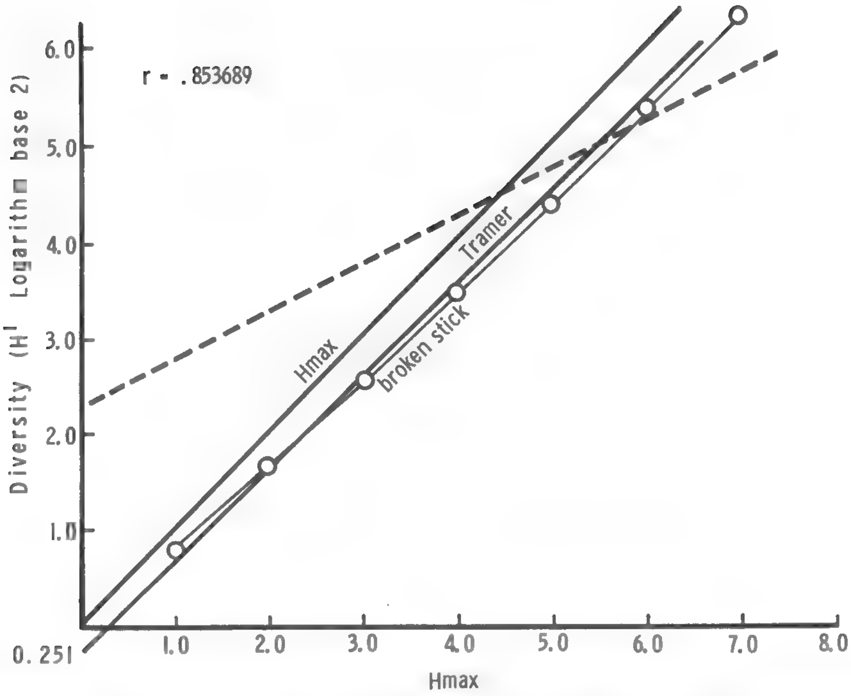


Figure 5. Regression showing changes in evenness of distribution of abundance as species number increases. The actual diversity (H' logarithm base 2) of Belém forest birds (dashed line) is compared with maximal diversity (all species being equally abundant, log 2 of the number of species). For comparison, Tramer's regression, based primarily on temperate censuses, is included. "A" line represents communities following the abundance distribution of the "broken stick" model (Appendix 1).

(*Eciton* sp.) in the area attracted many White-shouldered Fire-eyes (*Pyriglena leucoptera*). Both bird species occur abundantly in the sample of the first 100 birds, their relative abundances being twice the values in the total sample. As the Belém second growth includes some trees of 15 to 20 meters in height, one would expect the real species diversity to be higher than that for Perú, where the second growth was six to seven meters high.

The diversity index (H', base 2) for Karr's first 100 birds caught in his moist forest study area is 4.06, considerably below most Belém values except the two with sampling error (capoeira, or second growth, and terra firme-varzea transition at Station A) and the Igapó. The igapó subjectively appeared to be the least diverse of the mature Belém forest types, both in birds and vegetation structure.

The Preponderance of Rarity

One of the tantalizing aspects of tropical forest communities is the presence of many exceedingly rare species. The minimum adult abundance in a community for a sexually reproducing species, such as a bird, is two, but even abundances of one individual occur. We captured one adult male Rufous-capped Antthrush *(Formicarius colma)* a number of times at Station A from 5 April 1967 to 10 January 1969, but never netted a second individual of the species. Had there been a second individual of the species present, it would almost certainly have been caught, because the genus *Formicarius*, and antthrushes in general, show no tendency to develop net shyness or net avoidance, at least in the Belém region.

Karr (1971), defining a rare species as less than two percent of his sample, show such species represent 36.3 percent of the individuals in his moist forest sample and emphasizes that it is unwise to ignore such species from the point of view of community energetics. If one eliminates rare species defined in this fashion from the Mocambo data, only 10 of 75 species remain — the same as saying that in a community of 75 species the major portion of them will occur with relative abundances of less than two percent.

With tropical rain forest birds, a two percent ceiling is probably too high for a definition of rarity. Many species occur in samples as one or two individuals. The extent to which this occurs in Belém samples is shown in Tables 8 and 9. For data only from low nets, such species represent from 29.9 to 42.4 percent of all species caught and from 1.96 to 8.60 percent of all individuals in the sample. Considering data from all nets, these rare species represent 34.6 to 43.4 percent of all species captured and 2.31 to 7.62 percent of all individuals caught. Thus, a large number of the species in these communities are rare. This has special effects on the equitability (ϵ) or evenness (J and J′) component of diversity in these forest communities.

Since many indexes are unresponsive to rarity, numbers of very rare species present a problem when measuring diversity with H′. A number of people (i.e., Karr, 1971; Orians, 1969) dealing with tropical forest birds have noted this problem.

The inverse of Simpson's (1949) measure is somewhat more sensitive to rarity. It also has the advantage of liberating the investigator from log tables, but evenness measurements similar to J′ or ϵ are harder to grasp. Each index has its particular drawbacks.

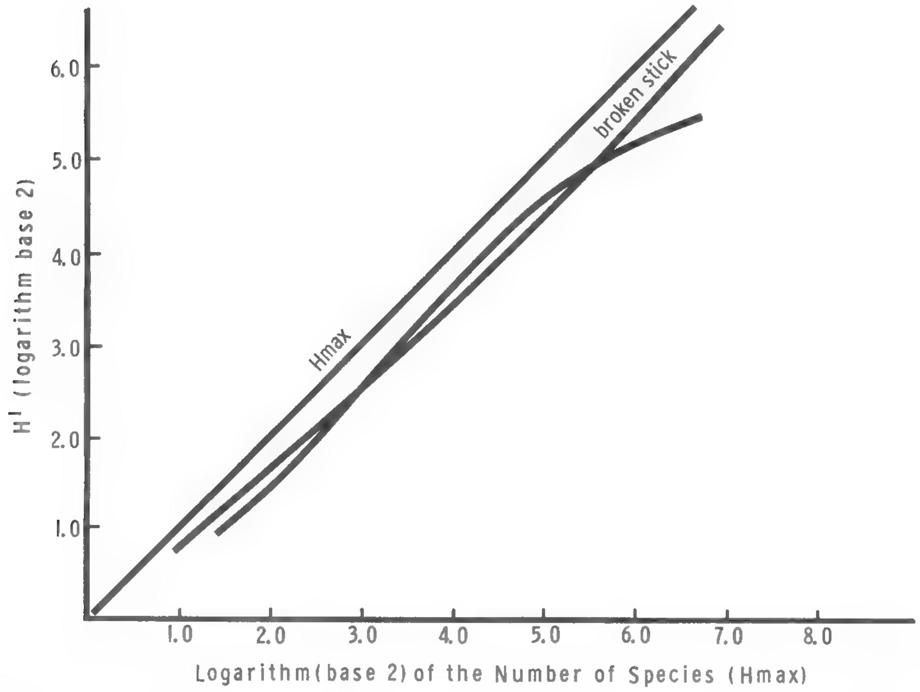


Figure 6. The change in evenness of distribution of abundance in bird communities as species number increases is shown by plotting diversity against the logarithm of species number. Evenness first increases as species number rises and then decreases. That curve is shown in relation to those for hypothetical communities corresponding to abundance distribution where all species are equally abundant (H_{max}). The curve for the broken stick model is also shown.

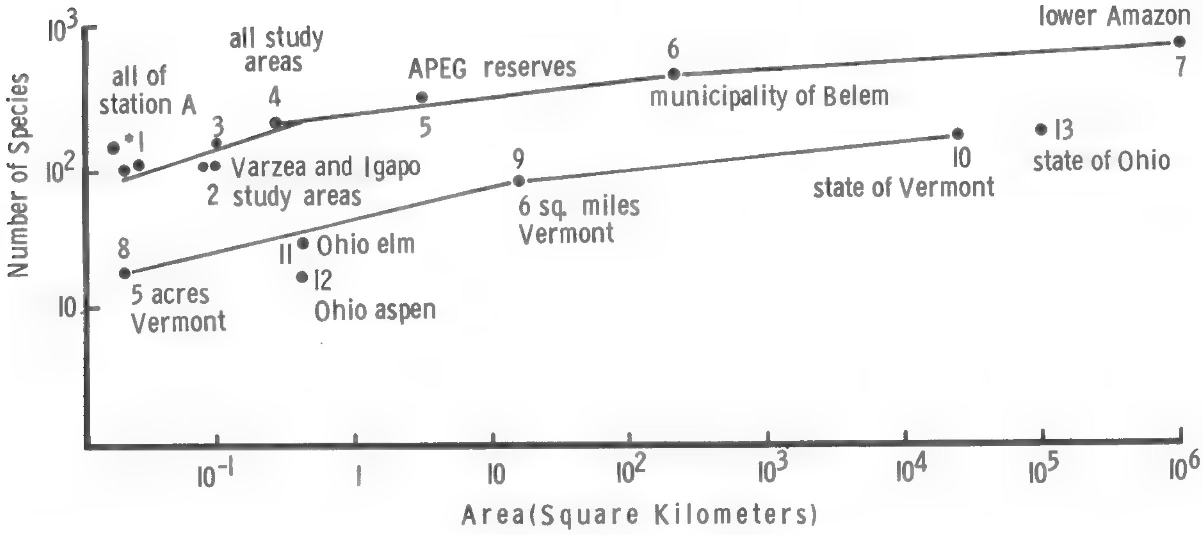
The Evenness or Equitability Component of Bird Diversities

That component of species diversity representing the distribution of abundance between species has been studied by a number of investigators, and recently by Tramer (1969) and Kricher (1972). This component is usually termed evenness or equitability and is defined as J′ or ϵ, respectively.

Each of these measures is defined relative to a specific pattern of abundance distribution, in the case of J′ relative to H_{max}, and in the case of ϵ relative to the broken-stick abundance model of MacArthur (1957). See Appendix 1. The latter model was proposed for theoretical reasons and later withdrawn (MacArthur, 1966), but is still useful as a pattern of abundance distribution.

Although the assumptions underlying the broken stick model are not the only ones leading to such a predicted distribution (Cohen, 1968), the distribution itself, for whatever reasons, does seem to occur in nature in some taxonomic groups under certain conditions. MacArthur (1960) demonstrated this distribution with some North American bird censuses from single (as opposed to mixed) habitats. King (1964) cited other groups fitting the broken stick distribution. More recently, Goulden (1969a, 1969b) and Tsukada (1967) have shown that this distribution is one toward which communities of chydorid Cladocera tend unless disturbed by pollution or other factors.

Calculations of equitability for Belém birds (Tables 10 and 11), however, demonstrate a less even abundance distribution than for the broken stick model. As this means a given number of species yields a lower value of H′ than if the distribution conformed to the broken stick, equitability values are less than 1.0. Reducing sample size by restricting data to those from low nets (Table 13) increases equitability values. Values range from 0.53 to 0.79 for data from all nets, and from 0.62 to 0.87 for data from low nets.



*1 2 to 3 hectare areas of Station A forests

Figure 7. Species area curves for the lower Amazon and the northeastern United States indicate the Amazon holds about five times as many species for an area of any given size. If geographic relief were comparable for the two regions, this tropical/temperate ratio would increase with area.

TABLE 7

Diversity of First 100 Birds Caught

	All nets[1]			*Low nets*		
	S	H'_e	H'_2	*S*	H'_e	H'_2
Belém:						
Station A						
Capoeria				25	2.56	3.70
Terra firme	33	3.07	4.43	33	3.07	4.43
Terra firme—varzea transition	33	2.76	3.99	35	2.80	4.04
Varzea	36	3.34	4.81	36	3.31	4.78
Mocambo				35	3.33	4.80
Varzea	38	3.41	4.91	33	3.23	4.66
Igapó	29	2.98	4.30	28	2.89	4.17
Peru:[3]						
Forest 1965				37	3.06	4.42
Forest 1966				31	2.85	4.11
Coffee I				29	2.99	4.31
Coffee II				29	2.89	4.17
Cacao				24	2.88	4.16
Second growth				30	3.08	4.44
Matorral				28	2.92	4.21

[1] Station A capoeira and Mocambo had only low nets.

[2] Letter headings indicate the following:
S = number of species
H'_e and H'_2 are a diversity index using logarithm base e and 2 respectively

[3] Data from Terborgh and Weske, 1969.

The equitability of Belém forest bird communities is shown graphically in Figure 4 where diversity (H′, base 2, abcissa) is plotted against the number of species (ordinate). The two lines showing exponential increase represent H′ for a broken stick distribution and H′ for the most even possible distribution (all species equally abundant), hence, H_{max}. As would be expected from the equitability values, all the points lie to the left of the broken stick distribution and increasingly so with more species. Most temperate North American bird censuses would fall on the line or very slightly to the left. This suggests there is a decrease in the evenness component of bird diversities in tropical rain forests.

Tramer (1969) working with J′ rather than equitability, demonstrated that diversity (H′) for 267 breeding bird censuses, including some tropical ones, is primarily a function of the number of species and that the pattern of relative abundance was fairly constant. This is in contrast to opportunistic species such as phytoplankton, which have been shown to vary primarily in the relative abundance component rather than the species number component of diversity (Sager and Hasler, 1969) or Caribbean corals, which vary in both components (Porter, 1972).

Tramer demonstrated the constancy of the relative abundance component for birds by calculating a regression which turned out to be

$$H' = 0.941 (H_{max}) - 0.251$$

The similar regression for the Belém data and Tramer's line are plotted in Figure 5 along with lines representing H′ for completely even abundance distribution, i.e., H_{max}, and H′ for a broken stick distribution. Tramer's line basically stays close to, but intersects, the broken stick line, implying a slight increase in equitability with increasing species number. J′ increases as well. The Belém line, however, suggests a decrease in J′ and equitability for species-rich situations of the neotropical rain forest.

The actual points in Tramer's plot suggest, if anything, that a curved-line fit would indicate a slightly accelerating increase in equitability and J′ with increasing species richness. Kricher (1972) found this to be true of bird communities of seral stages of the New Jersey piedmont. Tramer has few points for high species numbers, however. For tropical forests, his mean value for evenness (J′) is 0.921 (±0.012) and of species numbers is 55.14 (±11.24). The J′ value for his own census of Barro Colorado in 1969 is 0.823. Mean values for Belém forests range from 0.819 to 0.854, the lower values being for the largest samples that include all nets. These values are lower than the mean values of J′ for all of Tramer's habitat types except marshes, grasslands, and shrublands.

Values for Peruvian habitats (Table 12) taken from Terborgh and

TABLE 8

The Preponderance of Rarity
(Data from all birds caught in low nets)

	S[1]	S_1	S_2	N	N′	S_1+S_2/S (%)	N′/N (%)
Station A							
All habitats	128	31	9	2,495	49	31.3	1.96
Capoeira	100	27	14	898	55	41.0	6.12
Terra firme	66	15	9	507	33	36.4	6.51
Terra firme—varzea transition[2]	99	20	13	1,103	46	33.3	4.17
Varzea[2]	77	21	9	684	39	39.0	5.70
Mocambo (terra firme)	75	17	11	474	39	37.3	8.23
Varzea							
Total	87	22	4	1,112	30	29.9	2.70
Depressions	66	16	12	465	40	42.4	8.60
High ground	66	13	7	584	27	30.3	4.62
Igapó	93	33	6	1,088	45	41.9	4.14

[1] S and N are the number of species and individuals. S_1 is the number of species represented by one individual and S_2 is the number represented by two individuals; N′ is the total individuals of such species.

[2] Only data from net groups included, which omits data from one low net in the terra firme-varzea transition and five low nets in the varzea area respectively.

Weske (1969) are 0.847 for forest in 1965 and 0.831 for 1966 with values for secondary habitats ranging higher. Karr's moist forest sample from Panamá also yielded a low value (0.826). The Peruvian and Panamanian values are based on samples of 100 individuals only. The low values are in part due to the high abundance of a manakin species in each area. In contrast, Tramer's Barro Colorado census yielded only a seven percent relative abundance for the Red-capped Manakin, but abundance of this species varies greatly with distance from food sources and display areas. Had the samples been larger, the values would probably have been lower for reasons cited below.

Tramer (1969) and Kricher (1972) suggest, and MacArthur (1969) predicted, that when species are added to a community the extremes of abundance and rarity tend to become reduced. Tramer's data suggest that the tendency toward more evenness of relative abundance is a somewhat accelerating process as more species are packed into the community.

Once the number of species approaches levels of richness comparable to neotropical rain forests, a different phenomenon takes place because of the preponderance of rarity. As sample size increases, the relative abundance values of the more abundant species do not change appreciably, but new species represented by one, or perhaps two, individuals are continually being added. As sample size is increased, H_{max} thus is increasing, whereas H' hardly changes. Consequently, there is a decrease in J' and in equitability, whether one is increasing species number by enlarging the sample from the species rich community, or by sampling a yet even more species packed tropical community.

The high abundance of a manakin species in the studies by Karr (1971) in Panamá and by Terborgh and Weske (1969) in Perú is perplexing. Nomadism in both cases may be the cause. Four species of the same genus occur in the Belém forests but not one, nor all four together, constitute as

TABLE 9

The Preponderance of Rarity
(Data from all birds caught in all nets)[1]

	S[2]	S_1	S_2	*N*	*N'*	S_1+S_2/S (%)	*N'/N* (%)
Station A							
All habitats	161	43	14	3,078	71	36.0	2.31
Terra firme	104	30	13	735	56	41.3	7.62
Terra firme—varzea transition	110	24	17	1,206	58	37.3	4.80
Varzea	106	34	12	1,044	58	43.4	5.56
Varzea	125	30	18	1,767	66	38.4	3.74
Igapó	127	25	19	1,782	63	34.6	3.54

[1] Mocambo and Station A capoeira are not represented because they had only low nets.

[2] S and N are the number of species and individuals. S_1 is the number of species represented by one individual and S_2 is the number represented by two individuals; N' is the total individuals of such species.

large a proportion (ca. ⅓) of the total individuals in the community as in Perú or Panamá. James W. Porter and Geerat Vermeij (pers. commun.) suggest that Perú and Panamá have more seasonality than Belém, and this may somehow be related to the *Pipra* phenomenon. This high abundance as well as the rarity phenomenon would reduce J′ values.

Disregarding these two cases, the probable curve of changes in the relative abundance component of diversity with increasing species number can be described and is depicted in slightly exaggerated fashion in Figure 6. There is a slightly accelerating increase in evenness of abundance, becoming more even than the broken stick in the region of about 10 species, and the Belém data suggest there is an inflection point at about 30 or 40 species after which abundance distribution decreases somewhat in evenness. Thus, low equitability values for birds seem to be typical of both species rich and species poor communities.

Vertical Stratification

MacArthur *et al.* (1966) suggested that part of tropical species diversity was due to birds recognizing four layers of vegetation in tropical rain forests and only three in temperate forests. Empirically, just from the tremendous development of the canopy avifauna, there seems to be more vertical stratification of the birdlife in tropical rain forests than in the temperate forests.

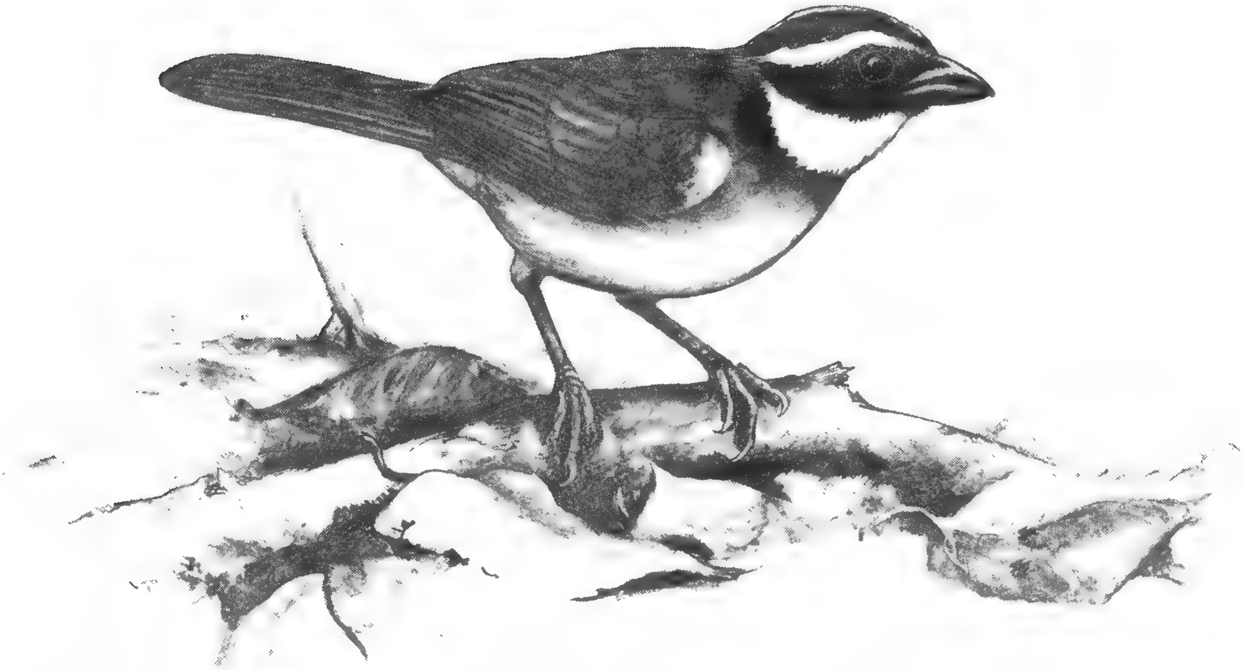
Terborgh and Weske (1969) used a rough but simple way of demonstrating vertical stratification of the birds in their forests by calculating the percent of the birds that were caught in nets set at ground level. As they noted, this value rises with increasing sample size; but as this is an asymptotic rise (increasing less abruptly as an upper limit is approached), the method is at least valid to demonstrate vertical stratification if not to provide a crude measure of it.

Terborgh and Weske found roughly one-third of the species known to occur were caught in low nets by the time the curve became highly asymptotic. This contrasted with 91 percent of the species in a mist net sample of 431 individuals in a Maryland study (Stamm, Davis, and Robbins, 1960). I did not calculate similar curves for Belém, but only slightly more than one-third of the known forest species were captured in low nets at Station A.

The data presented in Table 13 are not strictly comparable to the data of Terborgh and Weske, but nonetheless indicate the presence of vertical stratification of birds of the Belém forests. The percent of bird species caught in all nets that were also caught in low nets ranges from 63 percent to 90 percent. Had the denominator of these figures been the number of species known to occur in those forests rather than those which were caught, the values would have been lower. Also, had the numerator been chosen to be the number of species in the low-net sample when the species discovery rate was becoming asymptotic, the values would have been lower.

The high values are mostly a result of the relatively small number of birds caught in nets other than those set in usual fashion at ground level. High nets are more conspicuous because of the clearing around sites to prevent snagging; their low rate of capture is mostly attributable to this. The values reflect the simple statistical property that the greater the percentage of all individuals in the study that were captured in low nets, the larger the

Plain-throated Antwren, *Myrmotherula hauxwelli*. Drawing by John A. Gwynne, Jr.



Pectoral Sparrow, *Arremon taciturnus*. Drawing by John A. Gwynne, Jr.

percentage of all species that were caught in those nets. The igapó seems to be somewhat of an exception to this, probably because of all the forest types (Table 13), it was the most open and its avifauna seemed the least diverse.

The imprecision of this index for the reasons cited above does not permit comparative statements about stratification of birds in the various Belém forest types. The index does indicate the presence of vertical stratification, but detailed measurements still need to be made for tropical rain forest. Pearson (1971) has made these for a tropical dry forest and has similar data (*Ecology*, in press) for tropical rain forest.

Vegetation Structure and Bird Species Diversity

MacArthur and MacArthur (1961) showed that plant species diversity will predict bird species diversity in temperate regions but that a measure of structure, namely foliage height diversity (H′ of the proportion of foliage occurring in three layers), worked equally well. Furthermore, plant species diversity did not help to explain any of the residual variation in bird species diversity once the diversity of foliage height had been taken into account. Similar investigations of avian diversity have been largely restricted to the Western Hemisphere, although Recher (1969) and Blondel *et al.* (1973) conducted such studies in Australia and France, respectively. Recher (1971) recently published a general review of these sorts of studies.

How well does the diversity relationship work for tropical rain forests? Certainly, complexity of vegetation structure and bird species diversity are both very high. There are problems, however, with the use of foliage height diversity to predict bird species diversity for such environments. Initially, MacArthur *et al.* (1966) were able to resolve difficulties for some relatively small Panamá censuses by computing foliage height diversity for four layers instead of three. This seemed a reasonable approach since it was known empirically that there was greater vertical stratification of birdlife in tropical rain forests than in temperate forests.

Nonetheless, predictions of foliage height diversity based on the relationship found by MacArthur *et al.* (1966) seem to underestimate bird species diversity in neotropical rain forests (Lovejoy, 1972). Karr and Roth (1971) found this for Panamá moist forest, as did Terborgh and Weske (1969) for the forests of the Apurímac Valley in Perú, although part of the reason was that their samples were larger than MacArthur *et al.* (1966).

In addition, Pearson (1975b) found that foliage height diversity was very similar in three western Amazonian rain forests but that bird species diversity varied considerably in these forests. Conversely, in Peruvian habitats, Terborgh and Weske (1969) found very similar diversities of bird species in a variety of foliage height diversities.

If predictions are made for the large Belém samples on the basis of (1) four layers of vegetation with equal amounts of foliage and (2) the regression used by MacArthur *et al.* (1966), bird diversity (H′, base e) should be about 3.00, a considerable underestimate. If one could postulate more layers, this would then imply seven or eight layers of equally distributed vegetation.

Foliage height diversity is too crude a measure to predict bird species diversity in tropical rain forests. It cannot take into account the presence or absence of special structural features such as bromeliads, lianas, and other

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Wedge-billed Woodcreeper, *Glyphorynchus spirurus*. Drawing by John A. Gwynne, Jr.

TABLE 10

Evenness and Equitability of Belém Forest Communities (Data from all nets)[1]

	All birds					All birds except hummingbirds				
	H′ (base 2)	*S*	*S′*[2]	Σ (= *S′*/*S*)	*J′*	*H′ (base 2)*	*S*	*S′*	Σ	*J′*
Station A										
All habitats	5.82	161	85	0.53	.793	5.72	149	79	0.53	.791
Terra firme	5.76	104	82	0.79	.860	5.55	94	70	0.74	.847
Terra firme—varzea transition	5.62	110	74	0.67	.828	5.46	100	66	0.66	.820
Varzea	5.45	106	66	0.62	.810	5.50	96	68	0.71	.836
Varzea	5.60	125	73	0.58	.802	5.71	114	79	0.69	.836
Igapó	5.76	127	82	0.65	.824	5.80	117	84	0.72	.844
		$\bar{S} = 122 \pm 19.5$			$\bar{J}' = 0.819 \pm 0.022$		$\bar{S} = 111 \pm 18.8$			$\bar{J}' = 0.829 \pm 0.019$

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[1] Station A capoeira and Mocambo are not included as these areas had only low nets.

[2] S′ is the number of species necessary to give the value of H′, if relative abundances are distributed according to the type 1 broken stick distribution.

TABLE 11

Evenness and Equitability of Belém Forest Communities
(Data from low nets)

	All birds					*All birds except hummingbirds*				
	H′ (base 2)[1]	*S*	*S′*	$\Sigma (= S'/S)$	*J′*	*H′ (base 2)*	*S*	*S′*	$\Sigma = S'/S$	*J′*
Station A										
All habitats	5.71	128	79	0.62	.815	5.55	118	70	0.59	.806
Capoeira	5.45	100	66	0.66	.821	5.24	91	57	0.63	.805
Terra firme	5.24	66	57	0.86	.868	5.05	59	50	0.85	.859
Terra firme–varzea transition	5.58	99	72	0.73	.840	5.40	90	63	0.70	.830
Varzea	5.41	77	64	0.83	.863	5.26	68	57	0.84	.864
Mocambo (terra firme)	5.44	75	65	0.87	.873	5.26	67	57	0.85	.867
Varzea	5.48	87	67	0.77	.851	5.37	80	62	0.78	.850
Igapó	5.39	93	63	0.68	.824	5.18	83	54	0.65	.812

[1] Letters and symbols in the headings indicate the following:
S′ is the number of species necessary to give the value of H′, if relative abundances are distributed according to the broken stick distribution.
Σ = equitability, and J′ measures the evenness of abundance distribution.

epiphytes, as well as other factors of habitat quality (Terborgh and Weske, 1969). Orians (1969) studied a number of Costa Rican forests with a similar vegetation profile and found a wide range of bird species diversity mostly attributable to various qualitative characteristics of the different forests.

Aspects of habitat structure and habitat ecology that foliage height diversity can not measure apply to other environments, as well, as Carothers *et al.* (1974) demonstrated for cottonwood woodland in the southwestern United States and as Tomoff (1974) showed for desert scrub communities. Willson (1974) recently demonstrated a lack of correlation between foliage height diversity and bird species diversity in some Illinois forest sites.

Thus, although foliage height diversity is often sensitive enough to predict bird species diversity in temperate regions, it fails to do so for the complex neotropical rain forests. This does not mean a suitably sensitive measure of structural complexity would not better predict bird diversity in tropical rain forests; it undoubtedly would, but it might involve more effort than the demonstration would be worth. Nor does this negate the significance of physical structure of the habitat to avian ecology and diversity.

The seven or eight layers necessary to make foliage height diversity predict the bird species diversity that exists in Belém forests suggest the additional "layers" may represent various qualities of tropical forests not measurable by foliage height diversity but of considerable importance in contributing to bird species diversity. Among these are (1) the increased structural diversity and ecological opportunities represented by epiphytes and lianas, and (2) the year-round presence of food sources such as fruit (Morton, 1973), nectar, and large insects (Schoener, 1971), as well as a large lizard fauna and prey made available by swarming army ants. These are resources that are available to some degree throughout the year in tropical forests.

TABLE 12

Evenness and Equitability of Peruvian Bird Communities[1]

	H' (base 2)[2]	S	S'	$\Sigma\ (= S'/S)$	J'
Forest 1965	4.42	37	32	0.86	.847
Forest 1966	4.11	31	25	0.81	.831
Coffee I	4.31	29	29	1.00	.888
Coffee II	4.17	29	26	0.90	.858
Cacao	4.16	24	26	1.08	.905
Second growth	4.44	30	32	1.07	.905
Matorral	4.21	28	27	0.96	.876
					$\bar{J'} = .873$

[1] Data from Terborgh and Weske, 1969.

[2] Letters and symbols in the headings indicate the following:
S' is the number of species necessary to give the value of H', if relative abundances are distributed according to the broken stick distribution.
Σ = equitability
J' measures the evenness of abundance distribution.

The Horizontal Component of Diversity

According to the theory elaborated by MacArthur (1965), as habitats approach saturation with species, more species can move into a region if they exercise more precise habitat selection. This latter aspect of diversity is designated "between-habitat diversity" and can largely be measured for birds by the amount of change in avian community composition per unit change in vegetation structure. Karr and Roth (1971) found greater between-habitat diversity for mature habitats in Panamá than for temperate areas or immature Panamá habitats.

As I did not take appropriate measures of vegetation structure for the Belém study areas, I could not make a direct comparison. I tabulated the number of species caught in only one habitat to demonstrate the presence of this component of diversity. For these purposes I treated Mocambo and Station A terra firme as a single habitat and omitted data from the transition area between varzea and terra firme at Station A. The birds captured in these areas during the time interval of this study included 186 species and 53 of these, or roughly between one-fourth and one-third, were caught in only one forest type. The breakdown of this into the particular forest types is shown in Table 14 along with the numbers of species caught in two, three, and all four forest types.

Since I included only birds that were caught, species lists supplemented by observation would alter the results somewhat. Canopy species, as well as tinamous and trogons, are more widespread than the capture data might indicate. Furthermore, canopy species are probably less restricted to forest type, being more concerned with the uppermost surface of the forest than aspects below the canopy. It is possible that other species, unique to particular forests, might have been encountered.

Similar data are presented for pairs of forest types from Ohio, Illinois,

TABLE 13

Vertical Stratification

(Birds caught in low nets as opposed to all nets)

	N_1[1]	S_1	N_2	S_2	S_2-S_1	N_2-N_1	S_1/S_2	N_1/N_2
Station A								
Heterogeneous	2,495	128	3,078	161	33	583	79.5	81.1
Terra firme	507	66	735	104	38	228	63.5	69.0
Terra firme—varzea transition	1,103	99	1,206	110	11	103	90.0	91.5
Varzea	684	77	1,044	106	29	360	72.6	65.5
Varzea	1,112	87	1,767	125	38	655	69.6	62.9
Igapó	1,088	93	1,782	127	34	694	73.2	55.4

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[1] N_1 and S_1 are the numbers of individuals and species from low nets. N_2 and S_2 are the corresponding numbers for all nets. One low net for Station A varzea-terra firme transition and five low nets for Station A varzea are included in the calculation of N_2 and S_2 but not N_1 and S_1.

and Minnesota (Table 14), and are the same order of magnitude as those for the Belém forest types which have an average of 13.25 species unique to one forest type.

The explanation for the apparent similarity of magnitude for Belém and temperate forests is not totally clear. The large difference in structure between the coniferous (sclerophyll) bog forest and the broad-leafed oak forest in Minnesota most likely accounts for the large number of species unique to each. The Illinois late shrub and forest areas probably differ more in foliage profile than do Belém capoeira and terra firme because the Belém second growth has some fairly tall trees.

While the explanations for Illinois and Minnesota areas are reasonable, the Ohio situation is rather confusing. Ricklefs (pers. commun.) calculated the correlation coefficients between a variety of censuses, finding only one low value, and it involved this particular elm swamp, although he used data from a later census (Baker, 1958). The two Ohio areas are only about four miles apart and their foliage profiles must be rather close as indicated by the descriptions of the two areas.

Considering that this dissimilarity might be due to the wetness of swamp forest excluding ground nesting birds, I examined the nesting habits of the species involved. Of the 29 species in the elm swamp, only the Ruffed Grouse (*Bonasa umbellus*) is a ground nester. Of the 16 species in the dry ground forest, only the Ovenbird (*Seiurus aurocapillus*) is a habitual ground-nester (Headstrom, 1961). So the large turnover in species is not a result of the exclusion of ground nesting birds from the swamp forest. Furthermore, the swamp census included some species that are ground foragers such as the American Robin (*Turdus migratorius*) and the Common Flicker (*Colaptes auratus*).

With the exception of this rather mysterious pair of Ohio censuses, however, Belém forests seem to have more between-habitat diversity than some comparable north temperate forests. If, as well, the data from Panamá habitats are considered (Karr and Roth, 1971; MacArthur *et al.*, 1966), it is reasonable to suppose that appropriate vegetation measurements of the Belém forests will show a considerable between-habitat component of diversity.

The species-area curve for the Belém study areas, the reserves, the municipality of Belém, and the Lower Amazon is higher than the corresponding curve for Vermont (Figure 7), as would be anticipated from previous results (MacArthur, 1965, 1969; Preston, 1960). Points for Ohio show that a curve for this region would be about the same as for more mountainous Vermont. The Amazon and Vermont curves have similar slopes, indicating that a given area of tropical rain forest holds roughly five times as many bird species as an equivalent area in Vermont.

The relationship between the slopes of two species-area curves should not be used to indicate only differences or similarities in between-habitat diversity, as MacArthur (1965) and Karr (1971) have done, because this assumes areas of equivalent size to have an equivalent number of habitats. It is more valid to compare change in species composition per unit change of an appropriate physical component of the environment, such as foliage height diversity for birds. This avoids questions such as whether there are more habitats per unit area in the tropics.

The relationship of the slopes of the two curves can, however, indicate

TABLE 14

The Horizontal Component of Diversity

Number of species caught only in:	
Station A capoeira	8
Mocambo and Station A terra firme	14
Varzea	16
Igapó	15
Number of species caught in:	
One Belém forest	53
Two Belém forests	32
Three Belém forests	43
Four Belém forests	58
Number of species occurring in:	
Only one Ohio forest	29
Only one Minnesota forest	20
Only one Illinois forest	28
Two Ohio forests	8
Two Minnesota forests	12
Two Illinois forests	18

the amount of geographic subdivision of the avifauna in a region, particularly for areas greater than one hundred square kilometers. This need not relate directly to the amount of topographical variation in a region, such as the number of mountain ranges, although it will usually reflect this in part.

The Belém-Lower Amazon curve does not rise faster than the Vermont curve, whereas MacArthur's tropical curve (1969) does. One reason is the high number of species for Belém two-hectare areas. Probably, MacArthur's two-hectare census for Barro Colorado (MacArthur, *et al.*, 1966) is a considerable underestimate, in part because of the large territories of tropical rain forest birds (Karr, 1971). Nonetheless, the points for larger areas on MacArthur's tropical curve are valid, so his tropical curve shows more geographical subdivision than the temperate one, even if not at an increasing geometric ratio.

The Amazon curve would rise more rapidly than the Vermont one if the Lower Amazon had the amount of altitudinal variation such as occurs in Vermont and in the large tropical areas used by MacArthur. The main distributional barrier in the Lower Amazon for birds is the Amazon River itself and other rivers (Haffer, 1969; Sick, 1967). Rivers do not contribute as much of a geographical component to diversity as a mountain range, in part because of additional habitats added with altitude. In addition, altitude is more effective as a barrier in the tropics than in the temperate zone (Janzen, 1967). Consequently, if a correcting factor could be introduced, the avifauna of the Lower Amazon would show greater geographical subdivision (more species with non-overlapping ranges) than that of New England, and at an increasing multiple with greater area. This is what one would expect to find according to MacArthur (1965, 1969). Once within-habitat diversity approaches saturation level, between-habitat diversity begins to rise; and once the latter reaches some level, species are more readily added by geographic subdivision of a region. Between-habitat diversity, although not directly measured for the Belém forests, is high, and geographic subdivision has taken place. There must, of course, be opportunities for speciation to produce species for this accumulation process, such as Haffer (1969, 1970) proposed for Amazonian birds.

Increasing diversity by ever more precise habitat selection and geographic subdivision must, nonetheless, have its limits. This is probably reflected by spotty geographic distributions which seem to be a property of tropical communities (Diamond, 1973; MacArthur, 1969). For example, the Black-chested Tyrant *(Taeniotriccus andrei)* was caught in the Belém study areas about 500 miles east of the previous easternmost record on the Rio Tapajós.

Such distributions could be just a function of rarity and consequent probability of observation and are, actually, just part of a continuum of increasing rarity. These distributions could, however, be a real phenomenon with local extinctions and reinvasions constantly taking place. Diamond (1973) points out that low dispersal rates coupled with local extinction produce the patchiness of bird distribution frequently found in tropical rainforest. This is likely to lead to extinction of the species due to random fluctuations in the environment.

Total extinctions of species will happen less frequently if the area involved is very large, and random environmental fluctuations will be of less importance if there is considerable longevity providing more than a single chance to breed. The Lower Amazon is a large area and tropical passerines seem to have much lower adult mortality rates than temperate passerines (Snow, 1962a, 1962b; Willis, pers. commun.). It has recently been pointed out by a number of authors (Diamond, 1973; Elton, 1973; Lovejoy, 1973; and Terborgh, 1975) that tropical rain forest preserves and parks must be large to prevent local extinctions. Whether many more bird species could be packed into the Lower Amazon is an unanswerable question, but the spotty geographic distributions could be interpreted as suggesting a limit is being approached.

INTERHABITAT ABUNDANCE PATTERNS AND HABITAT TOLERANCE

The same bird species tended to be the most abundant in each forest type. In view of both the theory and results about between-habitat diversity in tropical regions, this was a sufficiently intriguing result to warrant further analysis. Consequently, I investigated the similarity of the most abundant species in the various forests. For comparison, I examined tree censuses, other tropical bird censuses, and some forest bird censuses from the eastern United States.

Distribution over a wide variety of habitats need not imply great abundance in any of the habitats. Nonetheless, this being a somewhat similar phenomenon, it was also examined for the Belém forest birds.

Methods

Tables of the absolute abundance (number of individuals) of the 10 most abundant bird species in each forest were compiled from data from all nets, and also from data just from low nets. In both cases, tabulations were made both with and without hummingbirds, to estimate the effect of the bias in the data with regard to this family of birds. Appendix 2 describes the methods for calculating the degree of similarity of abundant species in different forests as well as habitat tolerance ("niche breadth") of species.

It is important to be zoogeographically consistent in making such comparisons. For them to be meaningful, species should be absent from a census for ecological rather than zoogeographical reasons. There are, of course, cases where zoogeographical and ecological reasons for the absence of a species coincide. For example, the northern limit of the range of the Brown-headed Nuthatch (*Sitta pusilla*) on the eastern shore of Maryland and in Delaware coincides with the northern limit of the range of the loblolly pine (*Pinus taeda*), stands of which the nuthatch frequents.

Zoogeographical inconsistency has been avoided by choosing censuses very close to one another. The Belém censuses are all from the same ecological research area. The Ohio censuses are only four miles apart and the Minnesota censuses side by side. The Perú censuses are within two miles of one another in the same valley and the Panamá censuses are about nine miles apart. The Illinois censuses are within 35 miles of one another.

Results

The most abundant species tend to be the same ones in the various forests, as is apparent from the clustering in Tables 15 to 18. Deleting hummingbirds from the samples considered does not seem to affect the results substantially. High overlap occurs among the 10 most abundant species in the Belém forests (Figure 8), whether data from all nets or only low nets were the basis for the calculations.

The 10 most abundant species of trees tend to be different in all the Belém forest types (Table 19) except those forests that are essentially the same, such as high ground forest at Station A and high ground forest at Mocambo. The trees basically show low overlap (Figure 8), considerably less than for birds. At least seven pairs of forests showed no overlap at all. Overlap values for most of the other forest bird censuses are shown in Figure 9.

Niche breadth values for the 76 most frequently captured bird species are presented in Table 20. Figure 10 shows the relation of these values to frequency of capture. Niche breadth values for data from just the Igapó area are shown as a function of frequency of capture in that area in Figure 11. Both figures show a greater spread of values with higher frequency of capture although there are relatively few points for high frequencies of capture.

Figure 12 shows the number of species in different classes of niche breadth. There is a tendency for a greater number of species in smaller niche breadth classes except for the smallest size class.

Discussion

Effects of Biases in the Data on Overlap Values

The probable distortion of numbers of hummingbirds seems to have little effect on overlap values. In general, the highest values are lower in each case where hummingbirds are excluded, as some forest pairs may have an important hummingbird element in the 10 most abundant species. There is generally not, however, a major shift down in overlap values when hummingbirds are excluded.

The under-representation of canopy species would probably not affect the values, for most such species are not sufficiently abundant to rank

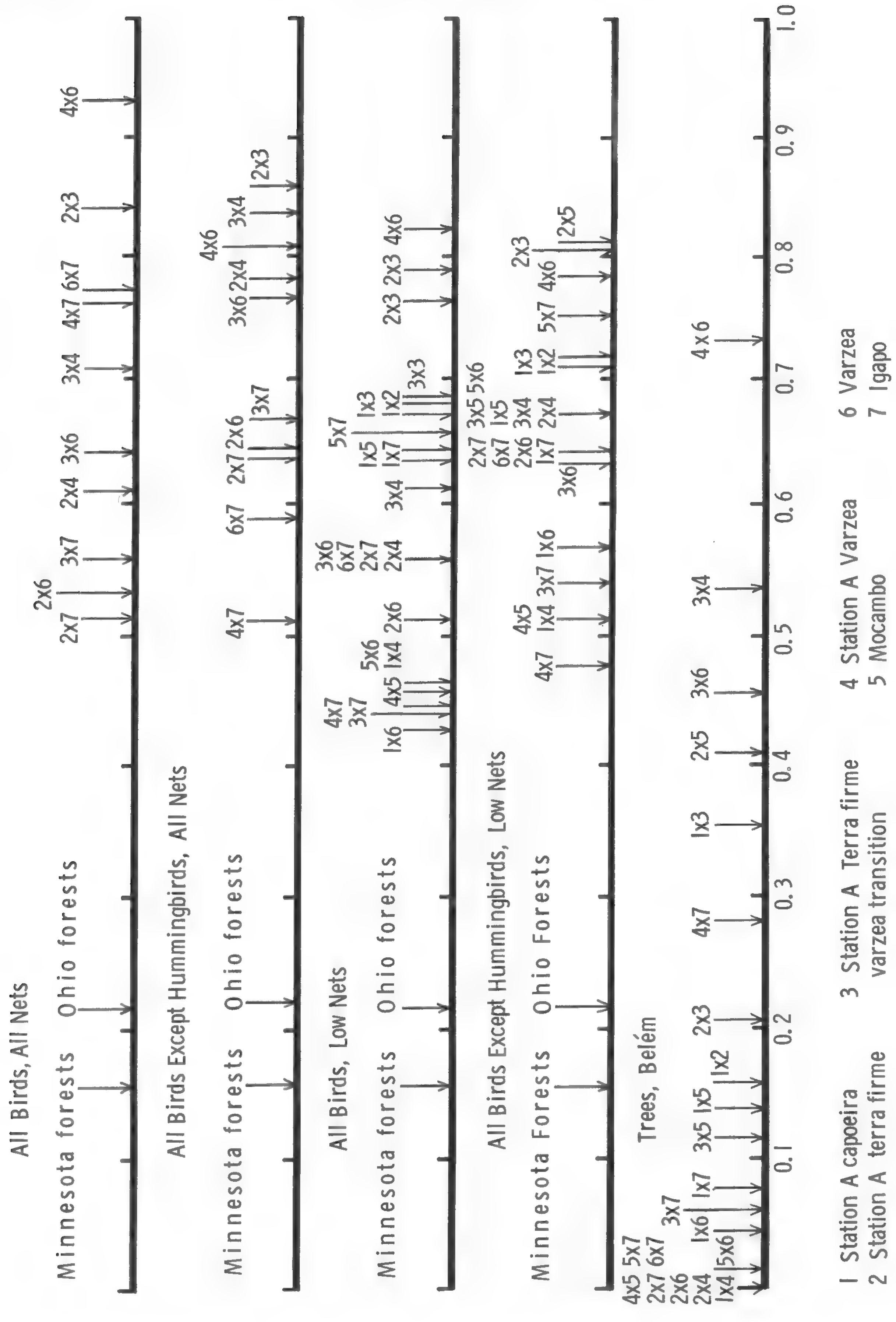

Figure 8. Overlap of the ten most abundant species is high for Belém bird communities as opposed to Minnesota and Ohio bird communities. The overlap is lower for Belém trees which are more affected by changes in the water table.

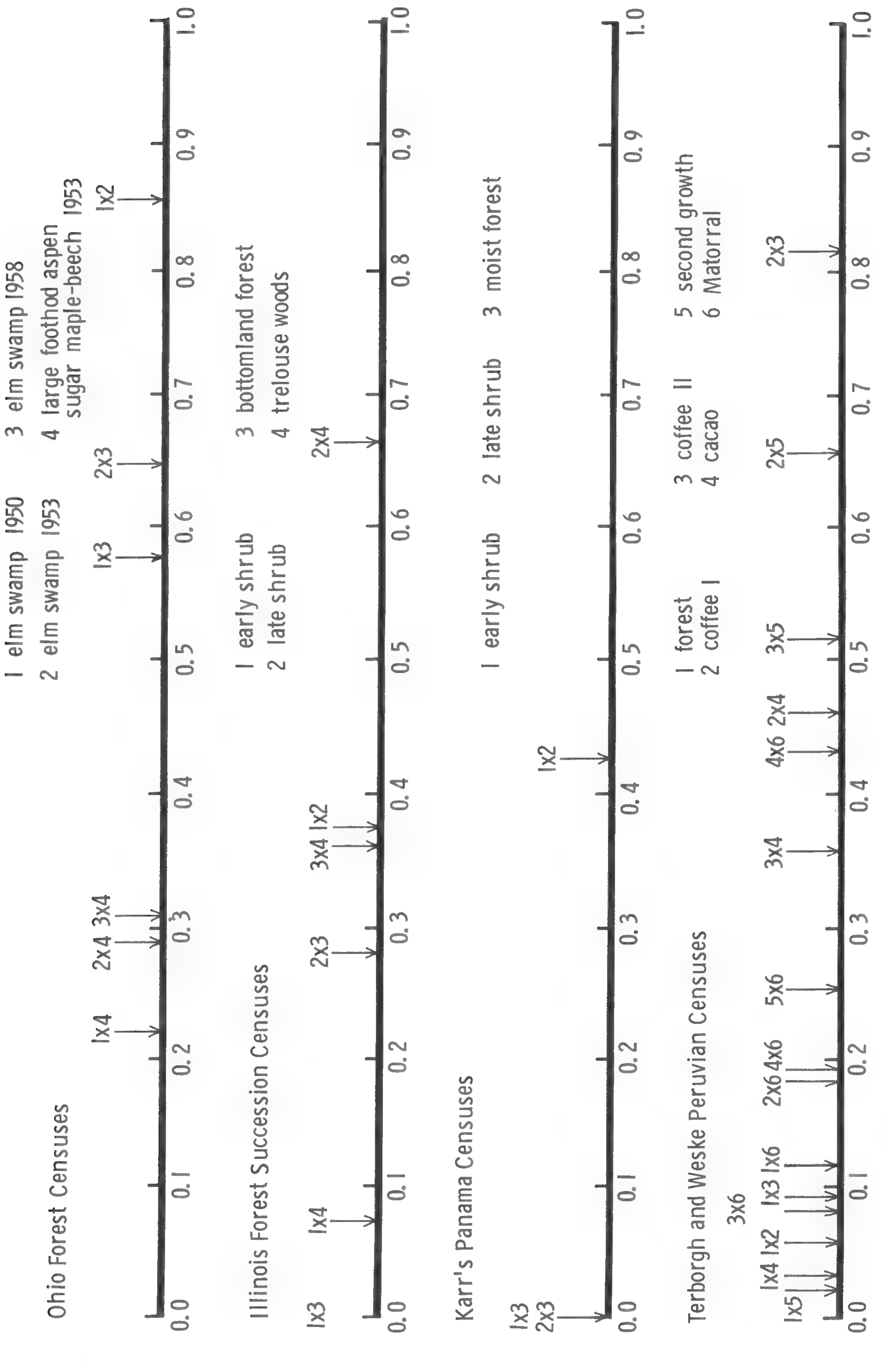

Figure 9. Overlap of the ten most abundant bird species is low for some Ohio bird communities. Overlap for abundant bird species of successional stages in Illinois, Panama, and Peru is consistently lower than for Belém (also see Figure 8).

among the top 10 in abundance. The canopy surface can vary extensively in height, forming green hills and valleys, and consequently canopy species forage over a large vertical range (Orians, 1969). The birds, however, interact more with a surface than with a three-dimensional habitat, and their home ranges are probably rather extensive. Some tanagers and honeycreepers possibly are abundant enough to rank among the 10 most abundant species, but these birds were poorly sampled in this study.

Net shyness does not affect the overlap calculations but net avoidance could result in a species being less abundant in the capture data than in reality. As far as it was possible to judge, net avoidance did not substantially affect which species appeared among the 10 most abundant; nor did it affect their numbers.

Overlaps of the Abundant Belém Forest Birds

Novaes (1970) listed the 10 most abundant species for three habitat types at Station A. These lists were based on data from low nets only, from once-a-week captures for a period of one year (May 1966 to April 1967). Novaes' varzea data are not strictly comparable, because they include what is considered varzea-terra firme transition in this study.

Using data from this study for low nets only, second growth (capoeira) results are similar to those of Novaes; the lists of 10 most common species have nine in common. For terra firme, there are only five in common and for varzea, eight in common. These differences would have given a high overlap value for a capoeira-terra firme comparison but not for any of the other two pairs. One can detect the similarity of abundant species between forest types, but really only in retrospect.

One result of the overlap comparison is the relatively small effect that vertical stratification seems to have on overlap. This may be due partly to the relatively small numbers of birds caught in high nets (Table 13).

Overlap values for low nets do tend to be lower than those for all nets, indicating that many of the most abundant bird species are not restricted to the ground and lower level of the forest (Figure 8). An average of six pairs of species are shared between forest types in the data from all nets; slightly less than five are shared for the same forest pairs in low net data. Thus, abundant species tend to be less confined vertically as well as horizontally.

It should be pointed out that overlap values are not meaningful for forests considered to be the same type on the basis of physical appearance. Not surprisingly, these forests are also similar in abundant tree species. The high overlap values for abundant bird species of such forests are thus to be expected on the basis of the relationship between bird species composition and tree species composition (Lovejoy, 1972).

Such forest pairs include Mocambo and Station A terra firme, and Varzea and Station A varzea. Similarly, there is a high degree of overlap for the Station A varzea-terra firme transition and the forest types it is transitional between, i.e., the varzea and terra firme portions of Station A. Likewise, one would expect a fairly high overlap between second growth (capoeira) and older dry ground forest at Station A and Mocambo.

Ignoring such forest pairs, we still find high overlap values between the 10 most abundant bird species in other forest pairs (Figure 8). This seems rather contradictory with the amount of between-habitat diversity that mature tropical habitats are supposed to have, and in fact do (Karr and Roth, 1971; Lovejoy, this study; MacArthur *et al.*, 1966). The paradox is explained by the behavior of the less abundant and numerous rare species, which are creating between-habitat diversity, while many of the more abundant species do not change very much from one forest to the next.

One possible cause of this high abundance of a species in more than one habitat is that mature birds may occupy the most desirable habitat while immatures are forced to exist in other, less desirable habitats. This need not put the immatures at a disadvantage, if the poorer habitat has sufficient resources to allow the immatures to maintain themselves although not enough resources to raise young. Among the abundant Belém bird species, the only obvious indication of such a phenomenon is the tendency for adult male Flame-headed Manakins (*Pipra rubrocapilla*) to occur in the middle and upper story of the forest, with females and immatures occurring lower. In this case, the upper reaches of the forest are preferred by the adult males for display areas. Therefore, the high overlap of the abundant bird species is not a consequence of different demographic classes occupying different forest types, but rather is probably due to some special characteristics of tropical forests, as I will discuss later.

The highest overlap values based on data for all birds from all nets occur for Station A varzea and the Igapó, and for the Varzea area and the Igapó. The overlap values for these two pairs drop to be the lowest values for all pairs when hummingbirds are eliminated from consideration. This presumably reflects the more open nature of these forest types, allowing hummingbirds, that might otherwise be more restricted to the upper strata, to penetrate lower into the forests.

Overlaps of the Abundant Belém Forest Trees

In contrast to the abundant bird species, the abundant tree species show low or zero overlap values between forest types (Figure 8). With the exception of the forests which are essentially the same forest type, overlap values range from below 0.375 to zero. This is quite similar to patterns elsewhere in the world including the temperate zone: edaphic situations have dominants different from those of the climax forest of a region. Swamp forests have different dominant species from dry ground forests, and various stages of regenerating forest have different dominants than mature forest.

If bird species composition is related to tree species composition (Lovejoy, 1972), and if the abundant tree species are very different in each forest type, it seems paradoxical that the abundant bird species remain much the same. This is explained, in part, by changes in the composition of the forest avifauna being mostly among the less abundant bird species. This phenomenon is also due to the composition of the forest, in which tree species change more rapidly over the environmental gradients than the inhabiting bird species, because the substrate of a forest is of more immediate importance to trees in terms of both support and nutrition. Birds, except for ground birds, can at least ignore the substrate in direct terms as a consequence of their powers of flight. Furthermore, if there are parts of a swamp forest which are not too wet, even ground birds are unaffected, whereas tree roots would still be affected by the high water table. Even army ants (*Eciton*), without powers of flight, can essentially ignore the

TABLE 15
Number of Individuals of the Ten Most Abundant Bird Species in Each Forest Type
(All birds caught in all nets)[1]

	Station A				
Species	*Terra firme*	*Terra firme—varzea transition*	*Varzea*	*Varzea*	*Igapó*
Wedge-billed Woodcreeper, *Glyphorynchus spirurus*	59	95	67	104	73
Ochre-bellied Flycatcher, *Pipromorpha oleaginea*	27	57	34	66	74
Pectoral Sparrow, *Arremon taciturnus*	*				85
Plain-throated Antwren, *Myrmotherula hauxwelli*	23	69	44	55	
Pale-tailed Barbthroat, *Threnetes leucurus*	21	41	124	217	210
Long-tailed Hermit, *Phaethornis superciliosus*	24		46	55	
Fork-tailed Woodnymph, *Thalurania furcata*		46	74	129	79
Ruddy Quail-dove, *Geotrygon montana*	26	36			
White-shouldered Fire-eye, *Pyriglena leucoptera*	47	53			81
Black-spotted Bare-eye, *Phlegopsis nigromaculata*				46	
White-flanked Antwren, *Myrmotherula axillaris*					65
Golden-headed Manakin, *Pipra erythrocephala*	51	105	73	71	46
Gray-breasted Sabrewing, *Campylopterus largipennis*			42		44
Cocoa Thrush, *Turdus fumigatus*			24	77	
Green-and-rufous Kingfisher, *Chloroceryle inda*			23		
McConnell's Flycatcher, *Pipromorpha macconnelli*	27				
Buff-throated Saltator, *Saltator maximus*	19				
White-necked Jacobin, *Florisuga mellivora*					59
Blue-backed Manakin, *Chiroxiphia pareola*				41	
Silver-beaked Tanager, *Ramphocelus carbo*		35			
White-crowned Manakin, *Pipra pipra*		35			

[1] Station A capoeira and Mocambo are not included as they had only low nets.

* Blank spaces do not indicate the absence of a species, but only that it was not one of the ten most abundant species in that area.

TABLE 16

Number of Individuals of the Ten Most Abundant Bird Species in Each Forest Type (All birds except hummingbirds caught in all nets)[1]

	Station A				
Species	*Terra firme*	*Terra firme—varzea transition*	*Varzea*	*Varzea*	*Igapó*
Wedge-billed Woodcreeper, *Glyphorynchus spirurus*	59	95	67	104	73
Ochre-bellied Flycatcher, *Pipromorpha oleaginea*	27	57	34	66	74
Pectoral Sparrow, *Arremon taciturnus*	*	27		37	85
Plain-throated Antwren, *Myrmotherula hauxwelli*	23	69	44	55	30
Ruddy Quail-dove, *Geotrygon montana*	26	36	18		
White-shouldered Fire-eye, *Pyriglena leucoptera*	47	53			81
Black-spotted Bare-eye, *Phlegopsis nigromaculata*	17	31		46	
White-flanked Antwren, *Myrmotherula axillaris*					65
Golden-headed Manakin, *Pipra erythrocephala*	51	105	73	71	46
Cocoa Thrush, *Turdus fumigatus*			24	77	
Green-and-rufous Kingfisher, *Chloroceryle inda*			23		
McConnell's Flycatcher, *Pipromorpha macconnelli*	27		19		
Buff-throated Saltator, *Saltator maximus*	19				
Blue-backed Manakin, *Chiroxiphia pareola*		34	21	41	
Silver-beaked Tanager, *Ramphocelus carbo*		35			
White-crowned Manakin, *Pipra pipra*		35			
Dusky Antbird, *Cercomacra tyrannina*					42
Silvered Antbird, *Sclateria naevia*					35
Pygmy Kingfisher, *Chloroceryle aenea*				37	32
White-shouldered Antshrike, *Thamnophilus aethiops*	14				
Blue-black Grosbeak, *Cyanocompsa cyanoides*			19		
Plain-brown Woodcreeper, *Dendrocincla fuliginosa*				39	

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[1] Station A capoeira and Mocambo are not included as they had only low nets.

* Blank spaces do not indicate the absence of a species, but only that it was not one of the ten most abundant species in that area.

substrate; although it was initially expected they would not occur in the igapó swamp, there is a sufficient quantity of fallen logs, vines, tangles, etc., for them to pursue their way of life above the black waters of the swamp.

Abundant Bird Overlaps of Belém and North American Swamp and Dry Land Forests

The overlap in abundant bird species between two pairs of North American forests is very low (Figure 8).

This is rather to be expected in the pair of Minnesota censuses, for the swamp forest is coniferous (tamarack and white cedar) and the dry ground forest is broadleaf (oak). With the large structural difference between sclerophyll and broadleaf forests, one would expect few bird species to be able to forage with equal success in both forest types.

In Ohio, the census of the upland forest (Figure 9) is compared with censuses of the elm swamp forest made in 1950, 1953, and 1958. The major difference in the swamp forest over this time was an increasing number of dying and falling elms. The overlap with the upland forest seems to increase — but not very much — as the swamp forest becomes more open.

There are no other comparable published data to show whether upland and swamp forest bird censuses in North America have characteristically low overlap in abundant bird species. Hence, it is hard to assess how much the Belém overlap is a result of the dry land-swamp comparison. Furthermore, those North American species with high niche width, as defined by McNaughton and Wolf (1970), are not those of greatest abundance (Ricklefs, 1972). The probable causes of the high Belém overlaps, discussed in the last section, suggest that the dry land-swamp nature of these overlaps is not an important factor.

Abundant Bird Overlaps in Successional Comparisons in Tropical and Temperate Areas

The degree of overlap of abundant bird species in early shrub, late shrub, and two mature forests in Illinois (Figure 9; Karr, 1968) is similar — between 0.3 and 0.4 for all pairs. A relatively high overlap occurs between late shrub and the Trelease Woods; the latter forest had a number of dead and fallen elms, and its more open nature made its similarity to late shrub greater than to the bottomland forest.

Karr (1971) censused early and late shrub habitats in Panamá that were as comparable in physiognomy as possible to his study areas in Illinois. He also censused birds in a Panamá moist forest, which is the most equivalent habitat to the mature Illinois forest he studied. The Panamá early and late shrub habitats had a fairly high overlap, 0.43, for the 10 most abundant bird species; but both shrub habitats had zero overlap with the moist forest. Terborgh and Weske's (1969) census for second growth and forest in Perú, where the overlap is a low 0.02, are probably most comparable to Karr's late shrub and mature forest censuses.

The early shrub-late shrub comparison gives a higher overlap for Panamá than Illinois but not much higher. That the Belém second growth terra firme overlaps are higher (both about 0.65 for Mocambo and Station A terra firme) than the Panamá and Perú areas may partly reflect the older age and taller stands of the Belém second growth. It is my impression from

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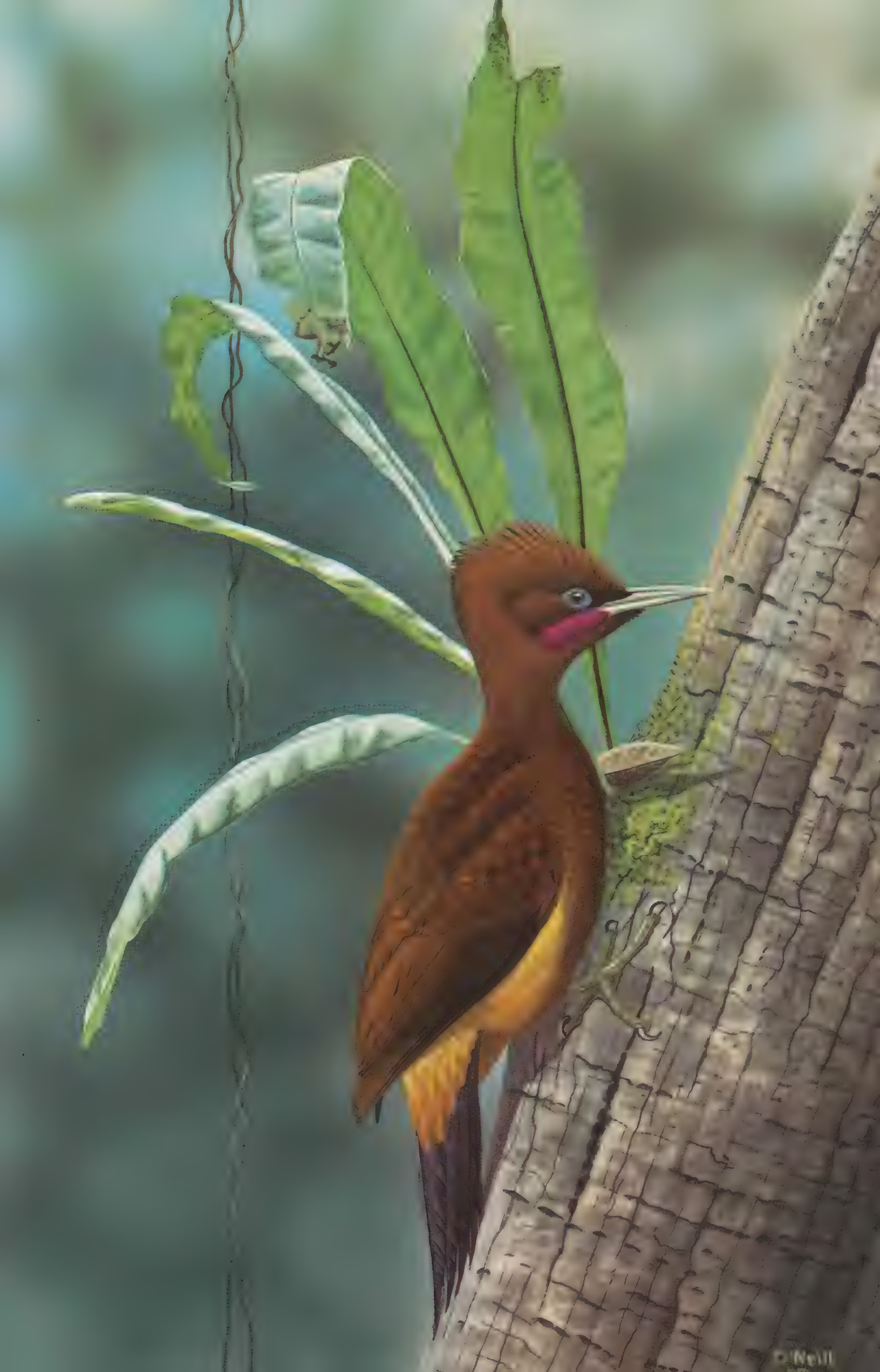
Plate II. Chestnut Woodpecker (*Celeus elegans jumana*). Painting by John P. O'Neill.


O'Neill

areas not on the APEG reserves that second growth of an age similar to the age of the Perú and Panamá forests studied would give lower overlap values with terra firme forest censuses than Station A second growth does; but it is difficult to assess whether the values would be as low as the Perú and Panamá results. It is not possible to reach any clear conclusion as to the degree of overlap of abundant bird species of tropical versus temperate forest successional stages.

Novaes (1970) pointed out that the 10 most abundant bird species in the second growth (capoeira) at Belém tended to be primary consumers (frugivores) whereas the species from taller forest tended to be on a higher trophic level. These results, however, seem mostly to be the result of his data being only from low nets. If hummingbirds may be considered as primary consumers, data from all nets show there to be seven primary consumers among the 10 most abundant species in all areas at Belém except the second growth, which has eight primary consumers. The other exception is Mocambo with only three primary consumers, but here data are available for low nets only. The impressive coevolution of epiphytes of the forest canopy and of flowering and fruiting trees with canopy birds results in a tendency for primary consumers to be more abundant in the upper portions of the tropical rain forests.

Comparisons with Other Neotropical Habitats

Censuses for neotropical forests similar to those at Belém do not exist in the literature. Censuses for a variety of secondary habitats in Perú (Terborgh and Weske, 1969), however, hint at higher overlap in abundant bird species for tropical as opposed to temperate forests. There are no zero overlap values in the 10 most abundant bird species between any pairs of the six censuses made, even though the cacao and coffee plantations were highly modified by man. The two coffee plantations, although differing a great deal in shade trees, had an overlap value of 0.83, almost as high as some of the highest Belém values.

These overlap values are based on mist net data only and so are most comparable to Belém overlaps calculated from low net data for all birds. Those are the lowest of all Belém overlaps because the abundant species tend to show no vertical restriction. This suggests that restriction of data to low nets may be responsible for the low overlap in the Peruvian studies involving the two primary habitats, forest and mattoral. All other overlaps are fairly high despite an isolation effect for some of the areas. Five or more of the 10 species are primary consumers, except for the mattoral with only four. It seems likely a pattern of high overlap of abundant species exists for these Peruvian forests as well as for Belém, with many of them being primary consumers.

Niche Breadth as a Measure of Habitat Specificity

Levins' measure of niche breadth (Appendix 2), when used as an index of habitat specificity or tolerance, has a number of imperfections. One difficulty is that the index reflects nothing of the qualitative differences between environments. Consequently, a given value of p_i (the proportion of a species' total frequency to be found in a single environmental type) contributes equally to the index whether that p_i is from an environment qualitatively

TABLE 17

Number of Individuals of the Ten Most Abundant Bird Species in Each Forest Type (All birds caught in low nets)[1]

	Station A						
Species	*Capoeira*	*Terra firme*	*Terra firme — varzea transition*	*Varzea*	*Mocambo*	*Varzea*	*Igapó*
Wedge-billed Woodcreeper, *Glyphorynchus spirurus*	83	56	93	64	34	80	68
Ochre-bellied Flycatcher, *Pipromorpha oleaginea*	50	20	55	32	16	55	68
Pectoral Sparrow, *Arremon taciturnus*	42	*			26	36	84
Plain-throated Antwren, *Myrmotherula hauxwelli*		23	69	44	28	52	
Pale-tailed Barbthroat, *Threnetes leucurus*				36		79	41
Long-tailed Hermit, *Phaethornis superciliosus*	34	19		28		37	33
Fork-tailed Woodnymph, *Thalurania furcata*			37	37		45	
Ruddy Quail-dove, *Geotrygon montana*		26	33				
White-shouldered Fire-eye, *Pyriglena leucoptera*	67	45	53		55		81
Black-spotted Bare-eye, *Phlegopsis nigromaculata*		17	31		16	46	
White-flanked Antwren, *Myrmotherula axillaris*							64
Golden-headed Manakin, *Pipra erythrocephala*	55	15	80				
Gray-breasted Sabrewing, *Campylopterus largipennis*				22			
Cocoa Thrush, *Turdus fumigatus*				20		62	
Green-and-rufous Kingfisher, *Chloroceryle inda*				23			
McConnell's Flycatcher, *Pipromorpha macconnelli*		25					
Buff-throated Saltator, *Saltator maximus*	28						
Silver-beaked Tanager, *Ramphocelus carbo*	33		35				
White-crowned Manakin, *Pipra pipra*			35		18		
White-shouldered Antshrike, *Thamnophilus aethiops*		14			13		
Blue-black Grosbeak, *Cyanocompsa cyanoides*	32			19	12		
Plain-brown Woodcreeper, *Dendrocincla fuliginosa*					10		
Pygmy Kingfisher, *Chloroceryle aenea*						36	32
White-bearded Manakin, *Manacus manacus*	62						
Dusky Antbird, *Cercomacra tyrannina*							41
Silvered Antbird, *Sclateria naevia*							35

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[1] Only net groups were calculated and those figures are used here; all low nets include only one more net for Station A terra firme-varzea transition and five more nets for Station A varzea than nets in net groups.

* Blank spaces do not indicate the absence of a species, but only that it was not one of the ten most abundant species in that area.

TABLE 18
Number of Individuals of the Ten Most Abundant Bird Species in Each Forest Type (All birds except hummingbirds caught in low nets)[1]

	Station A						
Species	*Capoeira*	*Terra firme*	*Terra firme—varzea transition*	*Varzea*	*Mocambo*	*Varzea*	*Igapó*
Wedge-billed Woodcreeper, *Glyphorynchus spirurus*	83	56	93	64	34	80	68
Ochre-bellied Flycatcher, *Pipromorpha oleaginea*	50	20	55	32	16	55	68
Pectoral Sparrow, *Arremon taciturnus*	42	13	*		26	36	84
Plain-throated Antwren, *Myrmotherula hauxwelli*		23	69	44	28	52	29
Ruddy Quail-dove, *Geotrygon montana*		26	33	17			
White-shouldered Fire-eye, *Pyriglena leucoptera*	67	45	53		55	31	81
Black-spotted Bare-eye, *Phlegopsis nigromaculata*	26	1	31		16	46	27
White-flanked Antwren, *Myrmotherula axillaris*							64
Golden-headed Manakin, *Pipra erythrocephala*	55	15	80				
Cocoa Thrush, *Turdus fumigatus*				20		62	
Green-and-rufous Kingfisher, *Chloroceryle inda*				23		33	
McConnell's Flycatcher, *Pipromorpha macconnelli*		25		18			
Buff-throated Saltator, *Saltator maximus*	28						
Blue-backed Manakin, *Chiroxiphia pareola*			30				
Silver-beaked Tanager, *Ramphocelus carbo*	33		35	16			
White-crowned Manakin, *Pipra pipra*			35		18		
Dutsy Antbird, *Cercomacra tyrannina*							41
Pygmy Kingfisher, *Chloroceryle aenea*				18		36	32
White-shouldered Antshrike, *Thamnophilus aethiops*		14			13		
Blue-black Grosbeak, *Cyanocompsa cyanoides*	32			19	12		

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[1] Only net groups were calculated and those figures are used here; all low nets include only one more net for Station A terra firme-varzea transition and five more nets for Station A varzea than nets in net groups.

* Blank spaces do not indicate the absence of a species, but only that it was not one of the ten most abundant species in that area.

similar to those in which the other individuals of that species occur, or from an environment qualitatively dissimilar, even though the latter case represents a truly broader habitat tolerance than the former.

Many species in tropical rain forest are rare and their distributions patchy. For these species, individuals are often found in extreme environments of the normal range and are missing from some intermediate ones. In more abundant species, distribution occurs along the full length of the gradient where the species normally occurs and an aberrational occurrence would receive a low p_i value and the index would not be distorted. The problems from this difficulty are, therefore, more likely to occur for rare species and have been somewhat avoided in these analyses by ignoring all species whose occurrence was recorded less than 10 times.

When dealing with a series of environments representing some sort of gradient, it is assumed that each successive environment differs ecologically as much from the previous one as its own successor does from it. One might, for example, study niche breadths of herbaceous vegetation along a transect running from a rocky hillside into a swamp. The assumptions arrived at are false if one defines the environments simply as 10-meter lengths of the transect. At the bottom of the hill, as the environment grades into swamp, the environment changes more rapidly than on the slope, but p_i values will not reflect this. Anticipating the problem by choosing shorter intervals in more rapidly changing areas will not solve the problem, because p_i values for these intervals will diminish with sample size. Choosing very small intervals over the entire gradient will not eliminate this problem, because regions of low gradient change are then represented by more "environments;" and species living in this part of the range will have relatively, and inappropriately, large niche breadths.

When dealing with samples taken along a transect, however, this problem can be partially solved by taking a constant number of samples for what one estimates as a unit of environmental change, although in a sense this is pre-judging the situation. One has to be so familiar with the ecology of the organisms involved to do this with accuracy that the answers to the exercise essentially would be known already. In practice, however, gross skewing of the results can be avoided by simply gathering a roughly similar number of samples from each habitat.

For this study, therefore, each forest type had a roughly equivalent number of net groups (Table 2). If similar environments are lumped, there are 20 terra firme net groups and 22 varzea groups, so there is some skewing. Species occurring in these two forest types will have somewhat larger niche breadth values than they should. Actual relative abundance figures, however, show most large niche breadth species are habitat tolerant.

It is also important for measuring and comparing niche breadth that the length of operation of each net-group be equivalent. This was essentially true, although Station A nets were opened a bit more frequently, and the Mocambo nets less frequently, than the others.

Measurement of niche breadth should be independent of relative abundance (Colwell and Futuyama, 1971) but this index is not. Rare species automatically have small niche breadths. For example, a species which only occurs 10 times in the data cannot have a niche breadth greater than 10 (or if one divides by n, a value of 0.13). More abundant species exhibit the possibility of a much greater range of niche breadth values. It is impossible, therefore, to distinguish between rarity *per se* and extreme habitat specificity. With calculations of relative abundance, one can determine which of the abundant species are habitat specific; but one cannot tell whether a species is rare because of a narrow habitat tolerance or whether it is rare for other reasons. This effect of rarity on the niche breadth index has been reduced somewhat by the restriction of the data to species caught 10 times or more.

Effect of Biases in the Data on Niche Breadth Values

The use of frequency data only from net groups affects niche breadth results. Canopy birds and the more abundant species are under-represented and have lower niche breadth values than in reality. Conversely, other species have somewhat larger values than they should because their vertical restriction was not taken into account.

Net shyness results in higher values of niche breadth than actually exist, because the curve that represents frequency of capture after development of net shyness is flatter, but as wide as the actual frequency of occurrence (Figure 3). Net avoidance, in contrast, results in values somewhat lower than the true ones, because the curve representing frequency of capture of species showing net avoidance is the same shape as that for true frequency, but lower and narrower.

Habitat Specificity and Tolerance of Belém Forest Birds

The niche breadth values for the 76 most abundant birds at Belém appear in Table 20 and are shown graphically as a function of abundance in Figure 10. The latter shows the effect of rarity on niche breadth values. Although there are few points for high frequency of capture, it is obvious

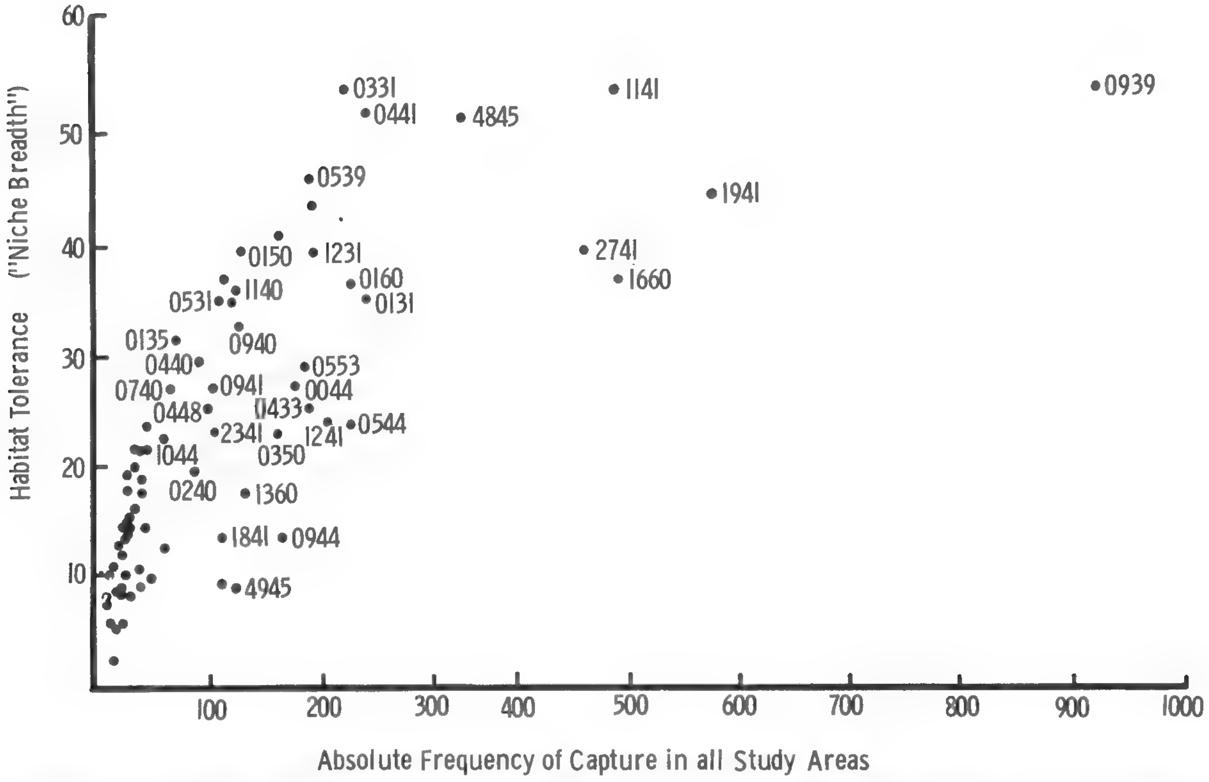

Figure 10. Habitat tolerance of Belém birds as measured by niche breadth is, in part, a function of absolute frequency. The greater the frequency of a species, the more a variation in habitat tolerance is possible. Species codes are given in Table 20.

TABLE 19
The 10 Most Abundant Tree Species in Each Forest Type in the Belém Study Areas

	Number of individuals	*Relative abundance*[1]		*Number of individuals*	*Relative abundance*
Station A capoeira:			Mocambo (terra firme):		
798 trees, 97 species			584 trees, 100 species		
Inga gracifolia	105	13.16	*Eschweilera odora*	68	11.64
Virma sp.	70	8.77	*Tetragastris trifoliata*	65	11.13
Pourouma sp.	58	7.27	*Eschweilera corrugata*	43	7.36
Tapirira guianensis	46	5.76	*Vochysia guianensis*	36	6.16
Eschweilera odora	37	4.64	*Vouacapoua americana*	21	3.60
Apeiba burchelli	32	4.01	*Goupia glabra*	21	3.60
Coroia exaltata	27	3.38	*Protium guacayanum*	20	3.42
Cecropia leoconima	19	2.38	*Tovomita stigmatosa*	19	3.25
Annona paludozia	15	1.88	*Protium paraense*	18	3.08
Socratea exorrhiza	15	1.88	*Micropholis acutangula*	16	2.74
	424	53.13		327	55.98
Station A terra firme:			Varzea (high ground):		
2,226 trees, 156 species			498 trees, 53 species		
Eschweilera odora	193	8.67	*Euterpe cleracea*	219	
Rinorea sp.	109	4.90	*Quararibea guianensis*	40	
Rinorea guianensis	68	3.05	*Pentaclethera macroloba*	32	
Cassipourea guianensis	62	2.79	*Inga gracifolia*	24	
Eronima sp.	57	2.56	*Carapa guianensis*	22	
Protium cuneatum	54	2.43	*Socratea exorrhiza*	12	
Pouraqueiba guianensis	51	2.29	*Tetragastris altissima*	12	
Theobroma subincanum	51	2.29	*Pouteria laurifolia*	8	
Cecropia obtusa	48	2.16	*Theobroma subincanum*	7	
Cecropia sp.	46	2.07	*Eschweilera odora*	7	
	739	33.21		383	

Station A terra firme-varzea transition:		
1,811 trees, 159 species		
Pentaclethera macroloba	129	7.12
Euterpe oleracea	87	4.80
Pourouma sp.	69	3.81
Tapirira guianensis	43	2.37
Theobroma subincanum	42	2.32
Eschweilera amara	39	2.15
Carapa guianensis	39	2.15
Inga gracifolia	38	2.10
Eschweilera odora	37	2.07
Protium cuneatum	36	1.99
	559	30.85
Station A varzea:		
569 trees, 62 species		
Euterpe oleracea	102	17.92
Pterocarpus amazonicus	38	6.68
Allantoma lineata	38	6.68
Pentaclethera macroloba	34	5.98
Caraipa grandiflora	27	4.75
Licania canescens	26	4.57
Licania heteromorpha	22	3.87
Carapa guianensis	21	3.69
Macrolobium pendulum	20	3.51
Symphonia globulifera	18	3.16
	346	61.01
Varzea (all net groups):		
1,115 trees, 67 species		
Euterpe oleracea	470	42.15
Astrocaryum murumuru	103	9.24
Quararibea guianensis	60	5.38
Pentaclethera macroloba	51	4.57
Licania canescens	48	4.30
Micropholis acutangula	40	3.59
Carapa guianensis	36	3.23
Inga gracifolia	31	2.78
Tetragastris altissima	18	1.61
Socratea exorrhiza	14	1.26
	871	78.11
Igapó (swamp):		
368 trees, 33 species		
Caraipa grandiflora	101	27.45
Pterocarpus amazonicus	41	11.14
Taralia oppositifolia	30	8.15
Tapirira guianensis	30	8.15
Bombax aquaticum	17	4.62
Symphonia globulifera	17	4.62
Ficus pulchella	15	4.08
Ambelania grandiflora	13	3.53
Virola surinamensis	11	2.99
Macrolobium bifolium	11	2.99
	286	77.72

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[1] Expressed in percentages.

that the more abundant a species is, the greater the range of niche breadth values possible.

The effect of rarity is not just a result of species being restricted to single forest types (Figure 11). Niche breadth values were calculated for capture frequencies in the igapó of the same species as shown in Figure 10, and were plotted against frequency of occurrence in the Igapó area. The plot is very much the same as in Figure 10, except for an even greater cluster of points at low frequency-low niche breadth values. Here the 76 species were included whether each had been captured 10 times or not. Thirty species were caught only once and had a resulting niche breadth of 1.0.

If one puts the various species into niche breadth classes of five units each, there is a definite trend for classes of smaller niche breadth values to hold more species (Figure 12). That this is not shown for the lowest class (values of 1.00 to 5.99) is an artifact of restricting the data to the 76 most abundant species. Had all the species been included, the lowest class would have been extremely high in species and the second to lowest class somewhat higher. These species might be rare because they have very rare habitats, and thus a low value of carrying capacity (K) per unit area; or they might be rare because they are far below their potential carrying capacity for a variety of reasons. One cannot distinguish between these two possibilities. The high number of rare or "habitat intolerant" species indicates a turnover in species from one forest type to another, as already indicated in the examination of between-habitat diversity.

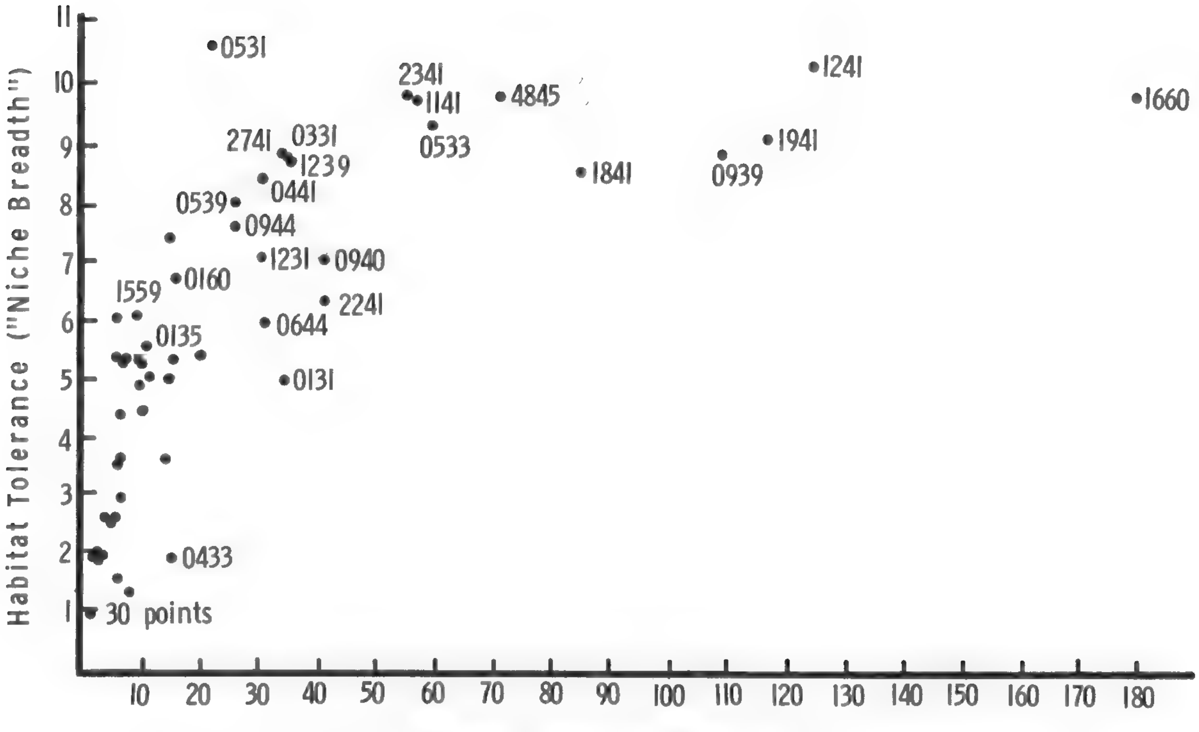

Figure 11. The relationship of habitat tolerance (niche breadth) to absolute frequency of birds from the Igapó study areas. Habitat tolerance is, in part, a function of frequency. Species codes are given in Table 20.

A number of species are habitat tolerant but never extremely abundant. Like the abundant species, these birds demonstrate the capability of being able to "ignore" differences in forest types. In this discussion, habitat tolerant species are those with values greater than 30.0, and are included in Table 21.

The Causes of Habitat Tolerance and Overlap of Abundant Bird Species

If a species has similar absolute abundance per unit area in two habitat types, both habitats offer the same basic niche requirements of that species. The various resources may differ in availability but the limiting factor, even if not the same in the two habitats, must be at the same level; other differences in forest type are irrelevant to such species. Differing abundance may be due to one or more of a number of factors.

The high overlap values in abundant bird species between forest types and their high values of niche breadth clearly indicate that many birds are able to ignore forest type. MacArthur (1960) stated that ". . . empirically, common species in one habitat are more likely than rare ones to be common or at least present in neighboring habitats." For Belém forest birds, however, the most abundant species tend to be the same in all forest types, presumably because the most abundant resources tend to be the most pervasive and persistent from one community to the next (McNaughton and Wolf, 1970).

The species with high niche breadths, however, are not all necessarily those most abundant in a forest type. Five of the 21 species with a broad habitat tolerance (>30.0) do not rank among the 10 most abundant species in any forest type, although they are ubiquitous and of about the same abundance in all forests. These species include the Black-faced Antthrush

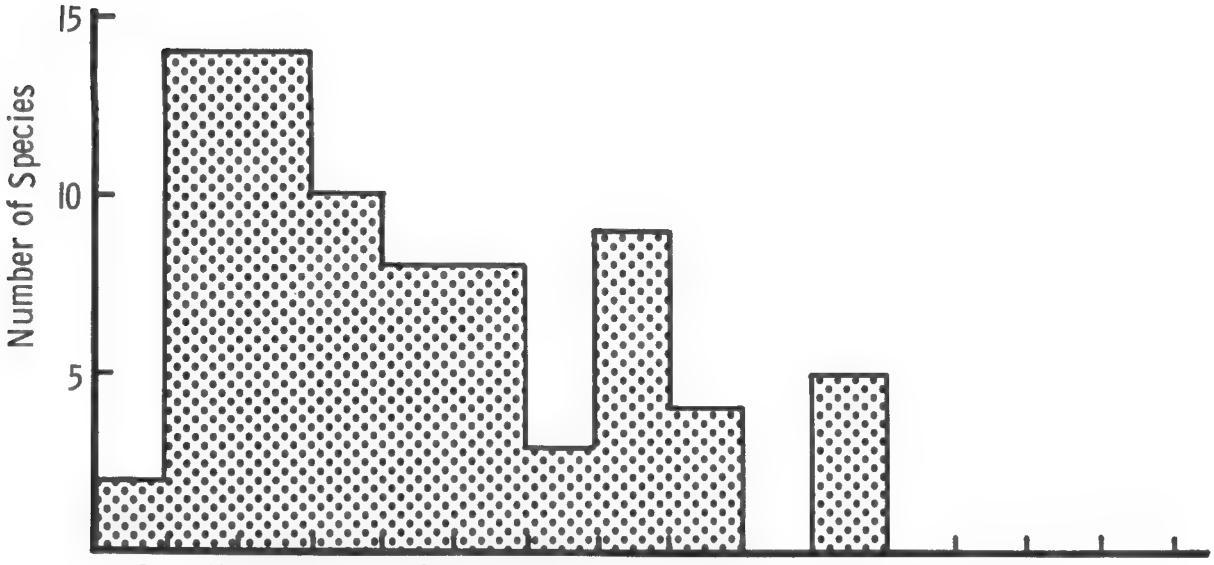

Figure 12. Habitat specificity of the most abundant Belém forest birds. Lower classes of habitat tolerance contain more species. This trend would be even greater if all species had been included.

TABLE 20

Habitat Tolerance (Niche Breadth) of the 76 Most Abundant Species

Species number[1]	Species name	Niche breadth	Species number	Species name	Niche breadth
0209	Barred Forest-falcon, *Micrastur gilvicollis*	14.7	1341	Long-winged Antwren, *Myrmotherula longipennis*	17.8
0823	Gray-fronted Dove, *Leptotila rufaxilla*	14.9	1441	Gray Antwren, *Myrmotherula menetriesii*	12.8
0923	Ruddy Quail-dove, *Geotrygon montana*	41.8	1841	Dusky Antbird, *Cercomacra tyrannina*	14.1
0131	Pale-tailed Barbthroat, *Threnetes leucurus*	36.0	1941	White-shouldered Fire-eye, *Pyriglena leucoptera*	44.6
0231	Rufous-breasted Hermit, *Glaucis hirsuta*	16.7	2241	Band-tailed Antbird, *Hypocnemoides maculicauda*	13.3
0331	Long-tailed Hermit, *Phaethornis superciliosus*	54.7	2341	Silvered Antbird, *Sclateria naevia*	24.0
0431	Reddish Hermit, *Phaethornis ruber*	11.0	2541	Black-faced Antthrush, *Formicarius analis*	37.1
0531	Gray-breasted Sabrewing, *Campylopterus largipennis*	35.8	2641	Scale-backed Antbird, *Hylophylax poecilonota*	16.2
0731	White-necked Jacobin, *Florisuga melivora*	9.8	2741	Black-spotted Bare-eye, *Phlegopsis nigromaculata*	40.4
1131	Blue-chinned Sapphire, *Chlorestes notatus*	12.4	0242	Ringed Antpipit, *Corythopis torquata*	17.9
1231	Fork-tailed Woodnymph, *Thalurania furcata*	39.9	0642	Bright-rumped Attila, *Attila spadiceus*	14.2
0433	Green-and-rufous Kingfisher, *Cloroceryle inda*	26.4	1143	Screaming Piha, *Lipaugus vociferans*	5.8
0533	Pygmy Kingfisher, *Chloroceryle aenea*	29.0	0344	Band-tailed Manakin, *Pipra fasciicauda*	21.8
0134	Blue-crowned Motmot, *Momotus momota*	6.5	0444	Opal-crowned Manakin, *Pipra iris*	8.9
0135	Yellow-billed Jacamar, *Galbula albirostris*	31.4	0544	Red-headed Manakin, *Pipra rubrocapilla*	24.0
0136	Collared Puffbird, *Bucco capensis*	11.0	0644	White-crowned Manakin, *Pipra pipra*	28.2
0636	Rufous-necked Puffbird, *Malacoptila rufa*	19.8	0844	Blue-backed Manakin, *Chiroxiphia pareola*	35.8
0538	Chestnut Woodpecker, *Celeus jumana*	14.5	0944	White-bearded Manakin, *Manacus manacus*	13.9

0139	Barred Woodcreeper, *Dendrocolaptes certhia*	22.2	1044	Thrush-like Manakin, *Schiffornis turdinus*	23.1
0439	Buff-throated Woodcreeper, *Xiphorhynchus guttatus*	15.2	2045	Ruddy-tailed Flycatcher, *Terenotriccus erythrurus*	19.3
0539	Spix's Woodcreeper, *Xiphorhynchus spixii*	45.8	2445	Royal Flycatcher, *Onychorhynchus coronatus*	22.2
0639	Striped Woodcreeper, *Xiphorhynchus obsoletus*	8.7	2645	Cinnamon-crested Spadebill, *Platyrinchus saturatus*	11.3
0939	Wedge-billed Woodcreeper, *Glyphorynchus spirurus*	54.3	3145	Rufous-tailed Flatbill, *Ramphotrigon ruficauda*	9.0
1139	White-chinned Woodcreeper, *Dendrocincla merula*	15.4	3645	Helmeted Pygmy-tyrant, *Colopteryx galeatus*	24.2
1239	Plain-brown Woodcreeper, *Dendrocincla fuliginosa*	44.3	4845	Ochre-bellied Flycatcher, *Pipromorpha oleaginea*	52.0
0240	Ruddy Spinetail, *Synallaxis rutilans*	10.3	4945	McConnell's Flycatcher, *Pipromorpha macconnelli*	9.0
0440	Cinnamon-rumped Foliage-gleaner, *Philydor pyrrhodes*	29.9	0448	Nightingale Wren, *Microcerculus marginatus*	26.3
0740	Olive-backed Foliage-gleaner, *Automolus infuscatus*	27.6	0150	White-necked Thrush, *Turdus albicollis*	39.2
0940	Plain Xenops, *Xenops minutus*	33.7	0350	Cocoa Thrush, *Turdus fumigatus*	23.4
1040	Tawny-throated Leafscraper, *Sclerurus mexicanus*	8.3	0255	Purple Honeycreeper, *Cyanerpes caeruleus*	2.5
1140	Short-billed Leafscraper, *Sclerurus rufigularis*	36.3	0356	River Warbler, *Basileuturus rivularis*	19.6
0441	White-shouldered Antshrike, *Thamnophilus aethiops*	52.3	1159	Silver-beaked Tanager, *Ramphocelus carbo*	9.6
0641	Amazonian Antshrike, *Thamnophilus amazonicus*	9.1	1459	Flame-crested Tanager, *Tachyphonus cristatus*	8.1
0741	Spot-winged Antshrike, *Pygiptila stellaris*	10.9	1559	Fulvous-crested Tanager, *Tachyphonus surinamus*	19.7
0841	Plain Antvireo, *Dysithamnus mentalis*	6.1	1659	Gray-headed Tanager, *Eucometis penicillata*	8.7
0941	Cinereous Antshrike, *Thamnomanes caesius*	27.4	0160	Blue-black Grosbeak, *Cyanocompsa cyanoides*	37.4
1141	Plain-throated Antwren, *Myrmotherula hauxwelli*	53.9	1360	Buff-throated Saltator, *Saltator maximus*	18.0
1241	White-flanked Antwren, *Myrmotherula axillaris*	24.1	1660	Pectoral Sparrow, *Arremon taciturnus*	38.3

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[1] The last two digits represent family number in taxonomic order from Tinamidae (= 01) to Fringillidae (= 60), and the first two digits represent species number within family. Hummingbirds (Trochilidae) are family 31.

TABLE 21

Relative Abundance of Habitat Tolerant Species in Net Groups[1]

			Station A				
Species	*Igapó*	*Varzea*	*Varzea*	*Terra firme—varzea transition*	*Terra firme*	*Mocambo terra firme*	*Station A capoeira*
HIGH ABUNDANCE							
Wedge-billed Woodcreeper, *Glyphorynchus spirurus*	7.1	9.4	11.7	9.5	12.1	8.0	10.6
Ochre-bellied Flycatcher, *Pipromorpha oleaginea*	7.4	5.4	5.8	5.6	4.3	3.4	6.4
Pectoral Sparrow, *Arremon taciturnus*	9.2	4.3	0.6	2.8	2.8	5.7	4.9
Plain-throated Antwren, *Myrmotherula hauxwelli*	3.1	5.6	8.0	7.1	5.0	6.7	0.9
Red-headed Manakin, *Pipra rubrocapilla*	1.6	1.3	2.6	8.2	3.2	2.3	7.2
Pale-tailed Barbthroat, *Threnetes leucurus**	3.3	6.8	5.3	2.7	1.2	1.5	2.0
Long-tailed Hermit, *Phaethornis superciliosus**	3.2	3.2	4.1	2.4	3.8	2.0	3.8
Fork-tailed Woodnymph, *Thalurania furcata**	2.6	4.4	5.4	3.4	1.4	1.0	1.3
Ruddy Quail-dove, *Geotrygon montana*	1.2	3.0	3.1	3.4	5.6	1.8	2.7
White-shouldered Fire-eye, *Pyriglena leucoptera*	8.8	3.6	1.5	5.4	9.7	12.9	8.8
Black-spotted Bare-eye, *Phlegopsis nigromaculata*	2.9	6.2	2.7	3.2	3.7	4.1	3.1
LOW AND INTERMEDIATE ABUNDANCE							
Plain-brown Woodcreeper, *Dendrocincla fuliginosa*	1.9	3.4	1.6	1.5	2.4	2.1	1.3
Spix's Woodcreeper, *Xiphorhynchus spixii*	1.5	2.3	2.2	1.6	1.9	1.8	1.3
White-shouldered Antshrike, *Thamnophilus aethiops*	1.9	2.6	2.0	2.0	3.0	2.6	1.2
Blue-black Grosbeak, *Cyanocompsa cyanoides*	1.5	1.5	3.5	2.6	2.4	3.1	4.1
Gray-breasted Sabrewing, *Campylopterus largipennis**	1.8	1.1	3.2	1.7	1.4	—	1.3
Yellow-billed Jacamar, *Galbula albirostris*	0.9	1.3	1.8	0.7	0.9	2.1	0.4
Short-billed Leafscraper, *Sclerurus rufigularis*	0.1	1.3	1.3	1.3	1.1	1.0	0.7
Plain Xenops, *Xenops minutus*	2.3	1.3	1.3	1.2	0.4	1.3	1.2
Black-faced Antthrush, *Formicarius analis*	—	1.1	1.5	1.5	1.9	0.8	0.5
Blue-backed Manakin, *Chiroxiphia pareola*	1.4	2.7	2.6	3.1	0.9	1.0	2.3
White-necked Thrush, *Turdus albicollis*	0.1	1.7	1.8	1.8	2.4	1.3	0.8
White-necked Jacobin, *Florisuga mellivora*	0.2	0.3	0.2	0.4	0.2	0.2	0.1

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[1] Values are for net groups excluding hummingbirds, except as indicated by an asterisk.

(*Formicarius analis*), a ground bird excluded from the igapó swamp but not from the varzea, the Plain Xenops (*Xenops minutus*), the Short-billed Leaf-scraper (*Sclerurus rufigularis*), the Yellow-billed Jacamar (*Galbula albirostris*), and the White-necked Thrush (*Turdus albicollis*).

Some species may rank in the 10 most abundant species in only one or a very few forest types, and as a result do not have niche breadths as great as 30.0. Some are typical of swamps: the Pygmy Kingfisher (*Chloroceryle aenea*), the Green-and-rufous Kingfisher (*Chloroceryle inda*), and the Silvered Antbird (*Sclateria naevia*). Others are found mainly in one forest type: the Cocoa Thrush (*Turdus fumigatus*) in varzea, the White-flanked Antwren (*Myrmotherula axillaris*) in igapó, and McConnell's Flycatcher (*Pipromorpha macconnelli*) in terra firme. Some are birds of openings and are well represented in second growth (capoeira): the White-bearded Manakin, the Silver-beaked Tanager, and the Buff-throated Saltator (*Saltator maximus*).

The canopy hummingbird, the White-necked Jacobin (*Florisuga mellivora*) is excluded, because I calculated niche breadth on data only from net groups as opposed to nets at all levels. The Flame-headed Manakin is not included for the same reason. Consequently, they are appropriately added to the list of habitat tolerant species, bringing the total to 23. A number of species are undoubtedly habitat tolerant but never sufficiently abundant to give a niche breadth value of 30. Such species probably include the White-crowned Manakin (*Pipra pipra*) and most canopy sepcies.

Why are these 23 species able to "ignore" forest types and why are they so abundant? For one thing, they are all small birds allowing greater numbers per unit of biomass. The largest species is the Ruddy Quail-dove (*Geotrygon montana*) which weighs about 130 grams; most are much smaller. The hummingbirds all weigh less than 10 grams, except the Gray-breasted Sabrewing (*Campylopterus largipennis*). The most generally abundant and ubiquitous species, the Wedge-billed Woodcreeper (*Glyphorynchus spirurus*), weighs about 14.5 grams.

Terborgh and Weske (1969) found, however, that families composed mainly of small species tend ot occur in only one primary habitat. Manakins were an exception to this and are represented by two species among the habitat tolerant species at Belém. Hummingbirds also probably are an exception. Terborgh and Weske (1969) pointed out the hopelessness of identifying hummingbirds in the forest canopy by sight.

Species on high trophic levels tend to be less abundant because of biomass considerations. In fact, the 23 species showing a high habitat tolerance are in low trophic levels, either being primary consumers or secondary consumers (insectivores).

Some of the species caught in nets are probably drawn from a larger area than others. This is true of species that follow army ant swarms. Always needing a colony in the nomadic phase, they must have a large area over which to roam. Manakins may also be drawn from a large area. With no male territories and a large population of immatures, there is a fair amount of wandering among manakins. It is my impression, however, that abundance values for these species were not unduly distorted.

It is tempting to regard these 23 species as "generalists," but niche breadth measures only habitat tolerance, and abundance measures only the success of a species in a forest type. Many of these species are, in fact, specialists in other aspects of their ecology, but specialists in sorts of things that enable them to ignore forest type. Many of the 23 habitat tolerant species exploit certain special characteristics of tropical rain forests. One of these is the presence of fruit all year (Orians, 1969), although not the same species, so that forests can support species that are obligate or predominant fruit-eaters such as manakins. This does not mean that fruit occurs with uniform abundance all year (Leck, 1972), but that it is always available (Smythe, 1970). Many fruits have small seeds and are dispersed by birds and other organisms. These fruits are more uniformly available through the year than those plants which do not depend on birds for dispersal. Indeed, selection probably favors staggered fruiting times of various species through the year to avoid competing for dispersal by birds, as Snow (1966) suggested for the plant genus *Miconia* (family Melastomaceae) in Trinidad. Other factors might also select for seasonality of fruiting (Leck, 1970); and some species feed on fruit only seasonally (Morton, 1973). Nonetheless, selection for dispersal includes selection of conspicuousness or self-advertisement in such fruits (Morton, 1973; Snow, 1971).

Fruiting the year around means flowering the year around, although the abundance of flowering varies. This makes it possible for forests to support many hummingbirds and other essentially obligate nectivores. Flowers that depend on hummingbirds for pollination have encountered selection for conspicuousness. Those that are insect pollinated are selected for conspicuousness, as well, although this conspicuousness will be somewhat different than that of hummingbird-pollinated plants, because of the nature of insect vision. Insects attracted to flowers will be easily found because of their association with such conspicuous objects. Twelve of the 23 habitat tolerant species are either mainly frugivorous or nectivorous, although they also feed on insects associated with the flowers and fruit (Table 22).

The presence of army ants (*Eciton* spp.) provides another special feature of tropical forests. In their nomadic phase, vast swarms of these ants move through the forest searching for insects, lizards, and other prey. The normally cryptic prey abandon their crypsis in attempting to flee. A number of birds habitually attend army ant swarms and prey on the conspicuous insect refugees. Willis (1967) defined a professional ant-following bird as one that depends for 50 percent or more of its food on prey fleeing from the ants. There are three such species (Table 22) among the habitat tolerant bird species of Belém forests. The ants are restricted to forests with high relative humidity, but not to a particular forest type. The three ant-following birds likewise are not restricted to any forest type. Thus, 15 of the 23 habitat tolerant species ignore forest types by using conspicuous foods peculiar to tropical forests.

Of the remaining eight species, seven seem to use substrates essentially the same from one forest type to the next. The Wedge-billed Woodcreeper searches for insect prey on tree trunks, and its larger relative, Spix's Woodcreeper *(Xiphorhynchus spixii)*, does the same. The Plain Xenops searches for insects on the outer limbs and twigs of trees. The Black-faced Antthrush searches the ground for insects. The Short-billed Leafscraper turns over leaves searching for insects. The Plain-throated Antwren (*Myrmotherula hauxwelli*) forages through tangles of vines and other vegetation in rather dark areas for insects. The White-shouldered Antshrike (*Thamnophilus aethious)* forages close to the forest floor for its insect prey.

Tree trunks and outer branches of trees are much the same from one

TABLE 22
The Ecological Classes of Habitat Tolerant Species

Nectivores

Pale-tailed Barbthroat, *Threnetes leucurus*
Long-tailed Hermit, *Phaethornis superciliosus*
Gary-breasted Sabrewing, *Campylopterus largipennis*
White-necked Jacobin, *Florisuga mellivora*
Fork-tailed Woodnymph, *Thalurania furcata*

Frugivores

Ruddy Quail-dove, *Geotrygon montana*
Red-headed Manakin, *Pipra rubrocapilla*
Blue-backed Manakin, *Chiroxiphia pareola*
Ochre-bellied Flycatcher, *Pipromorpha oleaginea*
White-necked Thrush, *Turdus albicollis*
Blue-black Grosbeak, *Cyanocompsa cyanoides*
Pectoral Sparrow, *Arremon taciturnus*

Ant-followers

Plain-brown Woodcreeper, *Dendrocincla fuliginosa*
White-shouldered Fire-eye, *Pyriglena leucoptera*
Black-spotted Bare-eye, *Phlegopsis nigromaculata*

Others

Yellow-billed Jacamar, *Galbula albirostris*
Spix's Woodcreeper, *Xiphorhynchus spixii*
Wedge-billed Woodcreeper, *Glyphorynchus spirurus*
Plain Xenops, *Xenops minutus*
Short-billed Leafscraper, *Sclerurus rufigularis*
White-shouldered Antshrike, *Thamnophilus aethiops*
Plain-throated Antwren, *Myrmotherula hauxwelli*
Black-faced Antthrush, *Formicarius analis*

forest to the next. So is the ground, except in igapó swamp forest where the antthrush is absent and the leafscraper occurs infrequently. The sorts of places where the antwren and antshrike forage probably differ but little in the various forest types.

It is significant that these 22 species mentioned search for food rather than pursue it. However one wants to define searching or pursuing (Cody, 1968; Schoener, 1969a, 1969b), there is a ratio of time or energy spent searching for food as opposed to pursuing it. If we considered time rather than energy, the search/pursuit ratio of ant-following species is also high. The twenty-third species, the Yellow-billed Jacamar, which sits quietly watching for insect prey to reveal itself and then darts out to catch it, likewise has a high search/pursuit ratio. It should be noted as well, that when the jacamar's prey reveals itself by moving, it is conspicuous. Thus, all 23 species search for their food; and for 16, the food is conspicuous.

It is probably difficult to pursue food with equal success in more than one type of forest. Different structure and differences in patterns of light and dark probably require different pursuit patterns and considerable visual flexibility (Karr, 1971). A number of species in tropical rain forests use the jacamar strategy of waiting for insects to reveal themselves, an effective strategy because of the relatively little wind in these forests (Orians, 1969). Some species, because they have low abundance, cannot be counted in the list of habitat tolerant species, and include a number of species using this strategy, such as puffbirds (Bucconidae) and some flycatchers (Tyrannidae).

Why then are the 23 habitat tolerant species the particular ones they are? Not all eaters of conspicuous food are either abundant or habitat tolerant. The answer for some of these species in part lies in the lack of competition from congeners in the Belém region. Not one of the five hummingbird species has a congener in Belém, although hummingbird genera are probably less distinct from one another than other bird genera (Sibley, 1957). One other genus (*Glyphorynchus*) is monotypic and seven others (*Geotrygon, Xenops, Pyriglena, Phlegopsis, Chiroxiphia, Cyanocompsa,* and *Arremon*) are represented by only one species in the Belém region.

Obviously, we need to learn a great deal more about the ecology of the Belém birds before we can know the full reasons for these particular 23 species being so habitat tolerant and so abundant. That there are such species partly reflects some unique properties of neotropical rain forests: conspicuous foods such as fruit, nectar, insects associated with flowers, animals fleeing from army ant swarms, and the fact that all these characteristics exist throughout the entire year.

Summary

Birds in four types of rain forest on the outskirsts of Belém, Brazil were studied in a banding program from 1967 to 1969. The roughly 15,000 captures of birds represent by far the largest sample of neotropical rain forest birds ever taken, and include for the first time almost all levels of the forest. Mist net data were used as the basis for all analyses and the possible biases in such data are discussed.

A variety of diversity indexes show these bird communities to be the most diverse ever recorded. A large number of the species banded were very rare, consisting of only one or two individuals in the sample. As a conse-

quence, the evenness, or equitability, of abundance distribution is rather low.

Bird communities with few species tend to have low equitability, but evenness of abundance distribution tends to increase with species number. Eventually, however, an increasing number of species takes place only by adding very rare species, and equitability decreases.

The Belém forest bird communities show vertical stratification and between-habitat diversity but neither have been precisely measured in this study. The species area curve for the Lower Amazonian avifauna shows greater geographical subdivision than a comparable north temperate area.

Foliage height diversity is too insensitive a measure to predict bird species diversity in forests as complex in structure as the ones in this study. It is necessary to postulate seven or eight layers of vegetation to make foliage height diversity predict bird species diversity in Belém. These additional "layers" may represent qualities unique to tropical rain forests such as army ants, epiphytes, lianas, year round fruiting and flowering, or a large lizard fauna.

There is a very high overlap in the 10 most abundant bird species between the various Belém forests. In contrast, a very low overlap occurs in abundant tree species. The abundant Belém bird species tend not to be restricted vertically as well as horizontally. Comparable dry ground-swamp forest comparisons in North America show low overlaps in abundant bird species.

Levins' index of niche breadth, despite a variety of imperfections, is used to measure "habitat tolerance." There are 23 habitat tolerant bird species in the Belém forests. Fifteen of these feed on conspicuous or "advertized" foods: fruits, the seeds of which are dispersed by birds (7 species); flowers dependent on birds for pollination (5 species); and normally cryptic prey fleeing from army ant swarms (3 species). Such foods are available all year long, which is not true of temperate forests.

The other habitat tolerant species use substrates, such as tree trunks, that are essentially the same in all forests. All 23 species search for, rather than pursue, their food. Searching for food should be easier in a variety of forest types than pursuing food, and is obviously even easier when the food is conspicuous.

The various results of this study emphasize some of the special qualities of tropical rain forests that should be borne in mind in generalizing from temperate to tropical forests.

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APPENDIX 1

Methods Used in Analyzing Diversity

I calculated a number of diversity indexes from the Belém capture data. These included the information-theoretic measure H′ (Shannon and Weaver, 1949), where

$$H' = -\sum_{i=1}^{s} p_i \log p_i$$

and p_i is the proportion of individuals in species i for all species 1 to s, and also Brillouin's index H, where

$$H = (1/N)\,(\log N! - \sum_{i=1}^{s} \log N_i!)$$

and N is the total number of individuals in a sample of s species and N_i is the number of individuals in the i th species. Stirling's approximation

$$\log n! \approx (n + 0.5) \log n - (\log e)(n) + \log \sqrt{2\pi}$$

was used in the actual calculations for the Brillouin index. A variety of logarithm bases has been used in the past with these indexes. In this case a base of 2 was used. This was the original log base used by Shannon and Weaver (1949) and also makes it simple to convert H′ into the equivalent number of equally abundant species. H′ was also calculated for base e for the sake of easy comparability with other studies.

A third diversity index was calculated for the bird data:

$$1/\sum_{i=1}^{s} (p_i)^2$$

where again p_i is the proportion of individuals in a sample of s species represented by species i. This is the reciprocal of the index originally proposed by Simpson (1949) and has been used by Levins (1968) and later MacArthur (1972) for some of the same purposes as H′. The relative abundance figures necessary to calculate this index and H′ are not presented but are available from the author or from University Microfilms (Lovejoy, 1971).

The diversity indexes were calculated for data from all nets, and from low nets. To gain some estimate of one of the biases in the data, calculations were made for the various sets of data both including and excluding hummingbirds.

As these diversity indexes reflect not only the number of species (S), or whatever entities are being measured, but also the evenness of the distribution of abundance amongst the species, it seemed appropriate to calculate a measure of this latter component as well. To measure the evenness of distribution of abundance it is useful to have some sort of constant pattern of distribution with which to compare the observed distribution.

For one such pattern, the ecologically absurd one in which all species are equally abundant, H′ is called H_{max} and it turns out that

$$H_{max} = \log_2 S$$

The ratio of the observed diversity and this quantity is

$$J' = H'/H_{max}$$

and provides an index of the evenness of distribution of abundance. This was calculated for all the capture data as well as for some data from the Amazon lowlands of Perú (Terborgh and Weske, 1969) and from Ecuador (Humphrey, unpubl. data). Means and standard deviations were calculated for each set of data.

Tramer (1969) examined J′ for 267 breeding bird censuses, calculating a regression line for H′ against H_{max}. A similar regression was calculated for the Belém data.

Another pattern is the "broken stick" distribution of MacArthur (1957). In this model of abundance distribution, the original assumptions were that the species did not overlap in their use of a continuum of resources, and that those resources could be represented in a linear fashion as if along a stick. Relative abundance of the n species was determined by randomly marking n–1 points on the stick and breaking the stick at those points, with each resulting piece thus representing the abundance of one of the species.

Relative to the broken stick pattern, Lloyd and Ghelardi (1964) proposed a method of comparing evenness of distribution, or as they termed it, equitability. For observed values of H′ for a given sample of s species, the same value of H′ exists for a broken stick distribution of s′ species. The measure of equitability is the ratio

$$\epsilon = s'/s.$$

This was calculated for all the capture data.

Karr (1971) and Terborgh and Weske (1969) calculated H′ for the first one hundred birds they caught in mist nets at ground level. For purposes of comparison, this was calculated for the Belém capture data for both low nets and all nets.

One aspect of tropical diversities is that many species are exceedingly rare. To provide an index of the extent of this phenomenon in the Belém birds, the number of species represented by only one or two individuals was tabulated and the percent calculated of (1) all species in a sample and (2) all individuals in a sample.

Vertical and horizontal aspects of diversity were also examined. Terborgh and Weske (1969) use a rough index of vertical stratification, namely the percent of species, known to occur in the forests, which were caught in low nets. This index was calculated for Belém birds and similar calculations using data from low nets as opposed to nets of all heights were made.

As measurements of foliage structure were not taken, a comparison of the amount of change in bird diversity with change in foliage configuration cannot be made. Although this measure of between-habitat diversity (Karr, 1971; MacArthur, 1965; MacArthur, Recher, and Cody, 1966) was consequently not available, a simpler way of demonstrating this was used. The number of species caught in only one forest type as opposed to two, three, four, etc., types was tabulated. Data for the two terra firme forests, Mocambo and Station A, were combined. Station A varzea-terra firme transition and varzea were not included as they are somewhat intermediate forest types. For comparison, a similar tabulation was made for two censuses in Ohio, an elm swamp forest

(Baker, 1950) and a large-toothed apsen-sugar maple-beech forest (Booth, 1953); for two censuses in Minnesota, a tamarack bog forest and an oak upland forest (Breckenridge, 1955); and for two censuses in Illinois, one a late shrub and the other a bottomland broadleaf forest (Karr, 1968).

A species area curve was constructed for the Lower Amazon and also for Vermont. Data from this study were used for the small area points. For the municipality of Belém, data are from a list compiled by P. S. Humphrey, F. C. Novaes, and myself; and for Lower Amazonia, data are from Griscom and Greenway (1941) to which 20 species are added to include ones discovered after 1941. Other data are from the following sources: five acres in Vermont, MacArthur and MacArthur (1961); six square miles in Vermont, MacArthur (1969); Ohio elm swamp, Baker (1950); Ohio aspen-maple-beech forest, Booth (1953); for the states of Ohio and Vermont, Peterson (1963).

The relationship of diversity of foliage profile and bird species diversity (MacArthur, 1964; MacArthur and MacArthur, 1961; MacArthur *et al.*, 1962; MacArthur *et al.*, 1966) is considered in the light of the diversity of bird species at Belém.

APPENDIX 2

Methods Used to Analyze Inter-habitat Abundance Patterns

Examination of tables for absolute abundance does not provide an easy grasp of the degree of similarity of abundant bird species between different forests. An index of similarity that could provide a quantitative measure was needed. Horn's (1966) index of overlap seemed appropriate. All birds caught in a forest that were in the 10 most abundant species were treated as a census, and the overlap index was

$$\frac{2 \sum_{j=1}^{n} (p_{ij})(p_{hj})}{\sum_{j=1}^{n} (p_{ij})^2 + \sum_{j=1}^{n} (p_{hj})^2}$$

with p_{ij} the proportion of species j out of the 10 most abundant species caught in forest type i, and p_{hj} the proportion of species j out of the 10 most abundant caught in forest type h. Since the total number of species in any two forests could vary from 10 to 20, depending upon the amount of overlap, for the formula to remain general, this number is referred to as n. Also, as this index measures the overlap in abundant species rather than the similarity of the complete censuses, a species that occurred among the top 10 of the one forest but not in a second, was counted as if absent from the latter forest.

For tropical comparisons, overlap values were calculated for data from Panamá (Karr, 1971) and from the Amazonian lowlands of Perú (Terborgh and Weske, 1969). For temperate comparisons, overlap indexes were calculated from bird censuses from two pairs of swamp and dry-ground forests, the tamarack-white cedar bog forest and upland oak forest pair in Minnesota (Breckenridge, 1955) and the pair in Ohio, consisting of a large-toothed aspen-sugar maple-beech forest (Booth, 1953) and an American elm swamp forest which was censused over a number of years as more and more elms died and fell. The earliest (Baker, 1950) and latest (Baker, 1958) censuses from the elm swamp forest were used as well as an intermediate one (Baker, 1953). To assess the similarity among abundant bird species in a temperate successional situation, as well as to compare with second growth and terra firme similarities in Belém, an overlap index was calculated from Karr's (1968) censuses for early shrub, late shrub, and bottomland forest areas in central Illinois. Karr included data for another forest, Trelease Woods, which had been censused by Barnett and Balda (1938) and an overlap index was computed with these data also.

Seventy-six bird species were caught 10 times or more among the various net groups, and to measure the degree of ubiquity of each of these species, niche breadths, as presented by Levins (1968), were calculated. This measure is the same as one used as a diversity index

$$1/\sum_{i=1}^{n} (p_i)^2$$

where p_i is, in this case, the proportion of a species occurring in environment i for all environments 1 through n. In this case, p_i is the number of captures (as opposed to individuals) of a species in net group i for net groups 1 through n (in this case 76).

It is somewhat deceptive to think of this measure as the breadth of a species' niche with its n-dimensions (Hutchinson, 1957). Rather, it seems preferable to think of this measure as an index of habitat tolerance in an ecological sense, enabling one to quantitatively measure the degree of habitat tolerance or habitat specificity of various species. This index has the property of being equal to n if a species is equally abundant in each of the n environments. The index is not directly comparable when measured in sets of environments of differing number. In order to make such comparisons, one must divide by the number of environments as Levins (1968) points out, i.e., niche breadth is then defined as

$$\frac{1/\Sigma(p_i)^2}{n}$$

As such comparisons are not being made, this modification has not been calculated and the highest possible value is 76.0 rather than 1.0.

This index is not independent of absolute abundance; and this relationship is examined by plotting niche breadth values against frequency of capture in all habitats and by plotting niche breadth values calculated just from igapó data against frequency of capture in igapó net groups. To measure apparent habitat specificity in Belém, the number of species in niche breadth classes of five units (or 0.068 if divided by 76) were plotted against these classes of niche breadth or habitat tolerance. Where possible, points on these scatter diagrams have bird species code numbers beside them. Species names and code numbers are listed in Table 20.

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Common Raven, *Corvus corax*. Painting by Tony Angell.

ACOUSTIC BEHAVIOR OF THE NORTHERN JACANA

DONALD A. JENNI, ROGER D. GAMBS, and BURR J. BETTS

The Northern Jacana (*Jacana spinosa*) breeds on floating vegetation in marshes, shallow lakes, river courses, and along the shores of larger lakes from southern Texas south to Panama. Its visual and vocal behavior are conspicuous to the human observer. Social interactions between adults almost always include vocalizations and sometimes appear to be restricted to vocal signals. Jacanas also use vocalizations in parent-young interactions and in anti-predator behavior. Non-vocal sounds do not appear to be an important part of the communication system.

The Northern Jacana is of special interest because it is the only species in which simultaneous polyandry is known with certainty (Jenni, 1974; Jenni and Collier, 1972). Males defend small territories; they exclude conspecific males, and although they attempt to exclude the much larger females, except for their mates, they generally fail to do so. Females exclude other jacanas of both sexes from the territories that belong to as many as four adjacent males. For the population on which we have the most complete records, each breeding female averages 2.2 males. However, there are always non-breeding adult-plumaged birds in the area, and we have no reason to suspect that the tertiary sex ratio differs from 1:1. Females maintain simultaneous pair-bonds with one to four males, and may copulate with all of them on the same day. Males perform all nest building, incubation, and care of the young. Oring and Knudson (1972) consider this system an example of "classic" polyandry. We are conducting a long-term study of the behavior of the Northern Jacana to understand how this species maintains polyandry and how it is adaptive. Eventually, we hope to gain insight into the evolution of polyandry in the jacana. In working toward those ends, we have started an intensive analysis of the Northern Jacana's behavior, part of which is the subject of this paper.

Most biologists studying vocal systems in birds describe calls and songs which, though variable, do not appear to overlap with one another. We do so below for the Northern Jacana. However, in producing sonograms of typical examples of the different calls, we became suspicious of our interpretation. We proceeded to prepare sonograms of all the sounds of the species that we recorded. We are now convinced that our original, subjective classification of jacana vocalizations is a naive over-simplification. We found a tremendous amount of variation in both individual note-structure and temporal patterning of the notes. In this paper, we will describe this relatively complex system.

Methods

Study Area

We made all the recordings at a shallow seven-acre pond near Turrialba, Costa Rica. The pond lies approximately 2,000 feet above sea level on the eastern or Caribbean slope of the Cordillera Central. Part of the shoreline is overgrown by papyrus (*Cyperus papyrus*), but floating water lily leaves (*Nymphaea ampla*) cover most of the lake. In recent years, intensive management of the lake has removed most of the other aquatic vegetation. This study area was described in detail by Jenni and Collier (1972). Additional field observations were made on jacanas in the provinces of Guanacaste and Puntarenas, Costa Rica.

Recording and Analysis

All recordings were made with a Uher, 4000 Report-L tape recorder using a Uher M514 microphone mounted on a plastic parabola. We recorded at seven-and-one-half inches per second on BASF Standard Tape (SP 52) during July and August, 1970, and May and June, 1972. We made additional observations in May and June of 1971 and 1973, and in January, 1971. Tape recordings were analyzed with a Kay 7030-A Vibralyzer. We regularly checked the frequency response of the machine against the manufacturer's samples and made necessary adjustments. We calibrated the speed of the recording drum (time axis of sonograms) by lightly inscribing the oscillations of a 100-hertz (Hz) tuning fork on smoked paper attached to the sonogram drum. Sonograms were made at the following settings: frequency range, 80 to 8,000 or 160 to 16,000 Hz; input impedence, 600 Ohms; record and reproduce volume unit levels, −10 to −5 decibels; high frequency pre-emphasis, H-S; automatic gain control, 1.0; mark level, 2.5 to 3.0. We made narrow-band and wide-band sonograms of all the calls and one-quarter speed logarithmic sonograms of many of them. All figures used to illustrate this paper are from high-contrast black-and-white photographs of narrow-band sonograms, but we measured note duration and inter-note intervals on the wide-band sonograms. In our analyses of individual notes, we relied heavily on the work of Greenewalt (1968), Marler (1969), and Stein (1968).

We color-banded most of the jacanas recorded and knew their roles in the social system (Jenni, 1974; Jenni and Collier, 1972). Notes on other aspects of the behavior of the vocalizing bird and other birds with which it was interacting were dictated directly onto the tapes. We transcribed these notes when the tapes were edited. We also recorded and made sonograms of other sounds at the lake so that we could identify them on the sonogram of jacana vocalization.

Results

Subjective Classification of Adult Calls

Northern Jacana vocalizations generally lack musical quality (pure tones). At first, the vocalizations seem to consist of a variety of relatively harsh notes that sound like variations of a squawk. Variation of notes occurs in length, temporal patterning, and acoustic quality. After we listened to jacanas call for some time, we felt that we could subjectively classify the calls into six relatively discrete calls. We then searched the tapes for calls that conformed to our subjective types.

Squawk. — Loud, relatively long (150–260 milliseconds [msec]) noisy calls. Sound energy is distributed over a wide range (0.5–6.5 kilohertz [kHz]). In some sonograms, the sound energy is more or less equally spread over a range of several kHz (Figure 1A). In other sonograms, the sound energy is concentrated in discrete bands. Squawks are given singly or in irregularly repeated sequences. Although the length of the notes often decreases during a sequence of Squawks, the note structure appears quite constant.

Scream. — Loud and relatively long sounds (Figure 1B), given singly or in short series. They appear less variable in duration (180–195 msec) than Squawks. Screams sound more piercing and higher pitched than Squawks. In Screams, the major sound energy is more concentrated (2.8–6.0 kHz) into two or three narrow bands, around 2.8, 3.5, and 5.6 kHz.

Strident Call. — A series of notes of short duration repeated at a relatively regular cadence (Figure 1C). This is the most frequent vocalization of the Northern Jacana. Although highly variable, Strident Calls usually include 10 to 45 individual notes. The variation among calls includes both the duration of notes and the intervals between them. Although these parameters also vary within any one call, the changes appear to occur progressively, rather than abruptly.

Duration of individual notes averages about 60 msec (20–143 msec); short notes are more frequent. The inter-note interval ranges from 37 to 213 msec. Intervals between the last few notes of a Strident Call often tend to increase slightly, and notes often become progressively quieter. Great variation appears in the structure of the individual notes that compose Strident Calls. Some of the notes are highly structured and appear to be composed of different frequencies produced alternately or produced at the same time with different components increasing, decreasing, or remaining stable in frequency.

Rattling Call. — Loud, short notes (24–61 msec) produced in rapid sequence with intervals between the first few notes becoming progressively shorter. Consisting of 10 to 28 notes, the calls end abruptly. Although the last inter-note interval may be longer, there is no progressive slowing of the cadence, as often occurs toward the end of Strident Calls. Generally, the acoustic energy covers a broad range, but often concentrates in one or more discrete areas, around 1.7 kHz and from 4.0 to 5.6 kHz (Figure 1D). The inter-note interval varies from 40 to 151 msec.

Chickety Call. — A repeated series of two to five, very brief notes (average about 30 msec, range from 16 to 65 msec), with a conspicuous pause between every group of two to five notes. The notes are structurally similar to some notes of Strident Calls, but more plaintive, quieter, and less harsh. The Chickety Calls appear to be emitted less frequently than the Strident Calls. However, since the Chickety Calls carry only about one-fourth the distance of Strident Calls, and are accompanied less frequently by conspicuous visual behavior, they may occur more frequently than our observations suggest. Jacanas most often arrange the notes of Chickety Calls in pairs and triplets (Figure 1E). In some notes, the acoustic energy is fairly evenly spread over a wide range (1.2–7.2 kHz). In the majority of notes, however, the energy appears to be concentrated in either, or both, of two discrete wide bands at about 3.0 and 6.0 kHz. Inter-note intervals range from 20 to 110 msec. Each group of two to five notes is separated from other groups of Chickety notes by periods of silence ranging from 82 to 291 msec. This temporal patterning makes Chickety Calls conspicuously different from other calls.

Flutter Call. — A series of 8 to 18 variable notes, some of which are similar to, but longer than the notes of Strident Calls. The inter-note interval is also longer (86–377 msec). Jacanas occasionally emit this distinct call while making a Flutter Jump into the air.

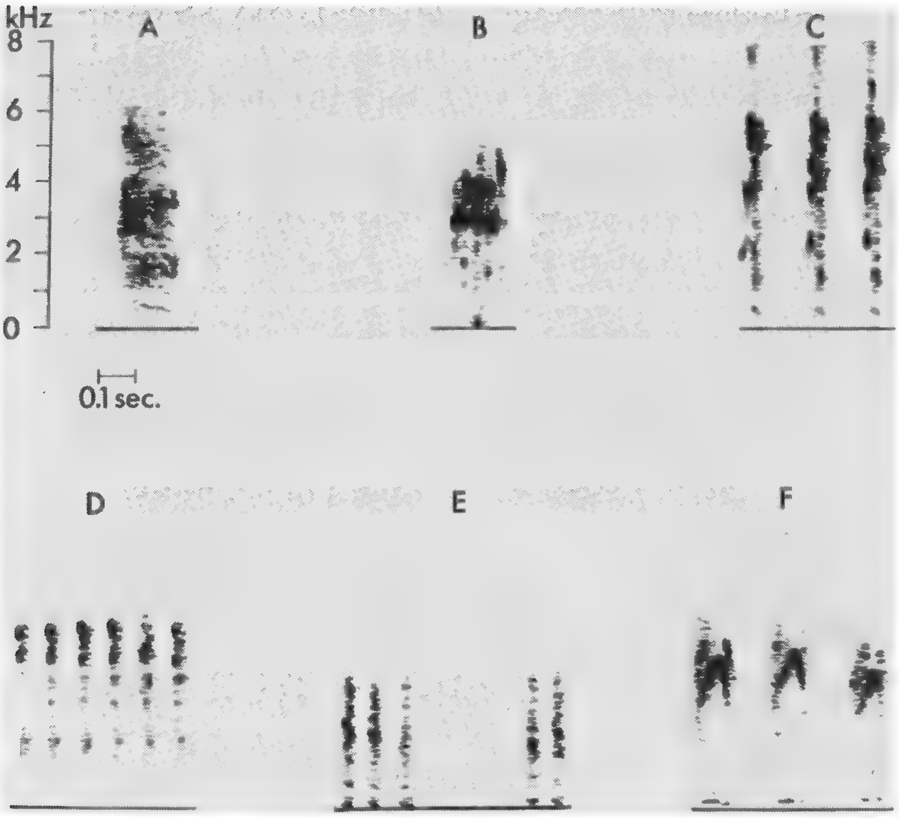

Figure 1. Selected sonograms of portions of the subjectively identified calls of adult Northern Jacanas. Notes are taken from the following calls: A, Squawk; B, Scream; C, Strident Call; D, Rattling Call; E, Chickety Call; F, Flutter Call.

Chick Vocalizations

Peep Call. — The only vocalizations of young Northern Jacanas recorded were series of Peep notes, which, although they vary (Figure 2), all sound very similar. Being simpler and lacking conspicuous harmonics, they differ markedly from notes produced by adults. Unlike adults, the young only rarely vocalize.

Sonographic Analysis of Individual Notes

In preparing sonograms to illustrate the subjectively identified calls, it became apparent to us that great variation occurs in the structure of notes, and that the variation does not appear to be related to call-type. However, these, too, were subjective impressions. To assess the variation in note structure in the Northern Jacana, we prepared sonograms of all our recordings (approximately 1,600) and analyzed them.

Individual notes differ from one another in temporal properties and frequency, which appear to vary independently. We made a large number of measurements of these parameters, but soon became convinced that such a quantitative analysis took us too far from the notes themselves, ignored much of the qualitative variation that seemed important to us, and did not significantly add to our understanding of the variation. Therefore, we turned to a qualitative analysis to describe note variation, relying heavily on the figures that accompany this article. In doing so, we ignored completely our earlier subjective classification.

We attempted to arrange individual notes in different continua. We tried using a variety of notes as starting- and as end-points and tried a wide variety of branching and recombining continua. After reviewing several possibilities, it appeared to us that the variation in note structure was best ordered by starting with a note that is long in duration and with the sound energy distributed more or less evenly over a wide frequency range (approximately 2.0 to 5.5 kHz). This relatively unstructured note is loud and noisy.

We tried to place each variant in a suitable place on a large flow chart so that each note, except the first and last of the various continua, appeared intermediate between the notes on either side of it. From this large and cumbersome array, we next selected a note from approximately the midpoint of each of the major continua and assembled an abbreviated diagram showing the major modifications of notes (Figure 3).

We must emphasize that this, and subsequent, flow charts (Figures 3, and 5 to 9) represent only our attempt to order the variation. They are not intended to represent ontogeny or phylogeny of note type and must not be interpreted as such.

The initial note (Figure 3A) appears to be a relatively unstructured sound that probably has a low fundamental frequency, which results in many harmonics (Greenewalt, 1968). The sound is probably modulated rapidly in frequency, producing many side bands and may also be rapidly pulsed (Stein, 1968). Notes possessing these qualities vary greatly in duration (Figure 4), with the shorter versions retaining the generalized nature of the long version.

Two different variations of this basic note form occur. Although there is some overlap between the two categories, sound energy may be either primarily pulsed (Figure 3, B and C) or primarily frequency modulated (Figure 3, D and E). Some notes appear on sonograms with visually discrete pulses, but it is difficult for us to hear any difference between the "basic note" and the rapidly pulsed ones. Throughout this paper, we use the term pulse to mean that, on the sonograms, the sound tracing shows temporally distinct increases and decreases in energy.

The dominant frequency of some primarily pulsed notes also may be frequency modulated; that is, the dominant frequencies of the individual

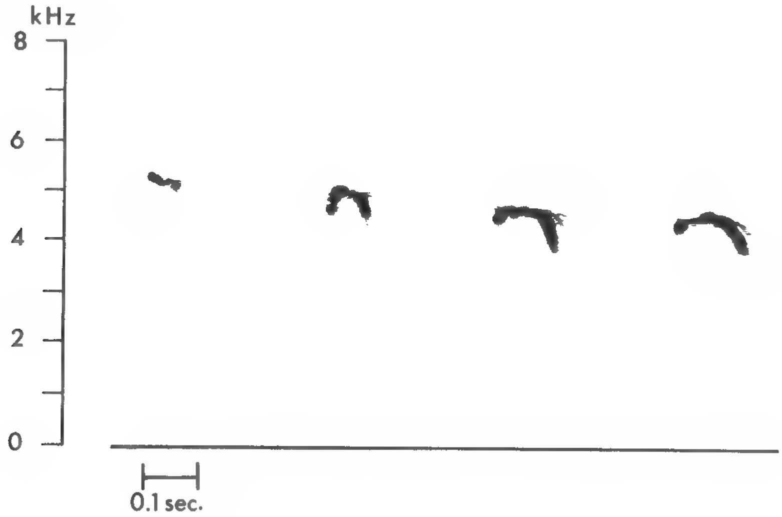

Figure 2. Peep vocalizations of a Northern Jacana chick.

pulses may be higher pitched in the middle portion of the note than at either end (Figure 5, first two notes in upper line). These notes also lack lower frequencies. It is difficult to see trends in shifting dominant frequencies in the last few notes of this continuum. Length of notes varies greatly. In shorter notes of this type, frequency banding becomes more prominent and there is rapid frequency modulation, especially in the prominent frequency zones. Our rationale for including these notes in this continuum is the presence of distinct pulses and the frequency modulation of what appears to be the dominant frequency. Rapidly pulsed notes, in which the notes retain the same dominant frequency through all the pulses, may be shortened by simply reducing the number of pulses per note (Figure 5, lower line). The shortest of these notes closely resembles the shortest note produced by simply shortening the basic note and may be identical (Figure 4).

Alternatively, the basic note (Figure 3A) may be modified by conspicuous frequency modulation with little or no pulsing (Figure 3, D and E). Such notes include conspicuous harmonics or spectral bands. Notes with four or fewer harmonics or spectral bands (Figure 6) differ from one an-

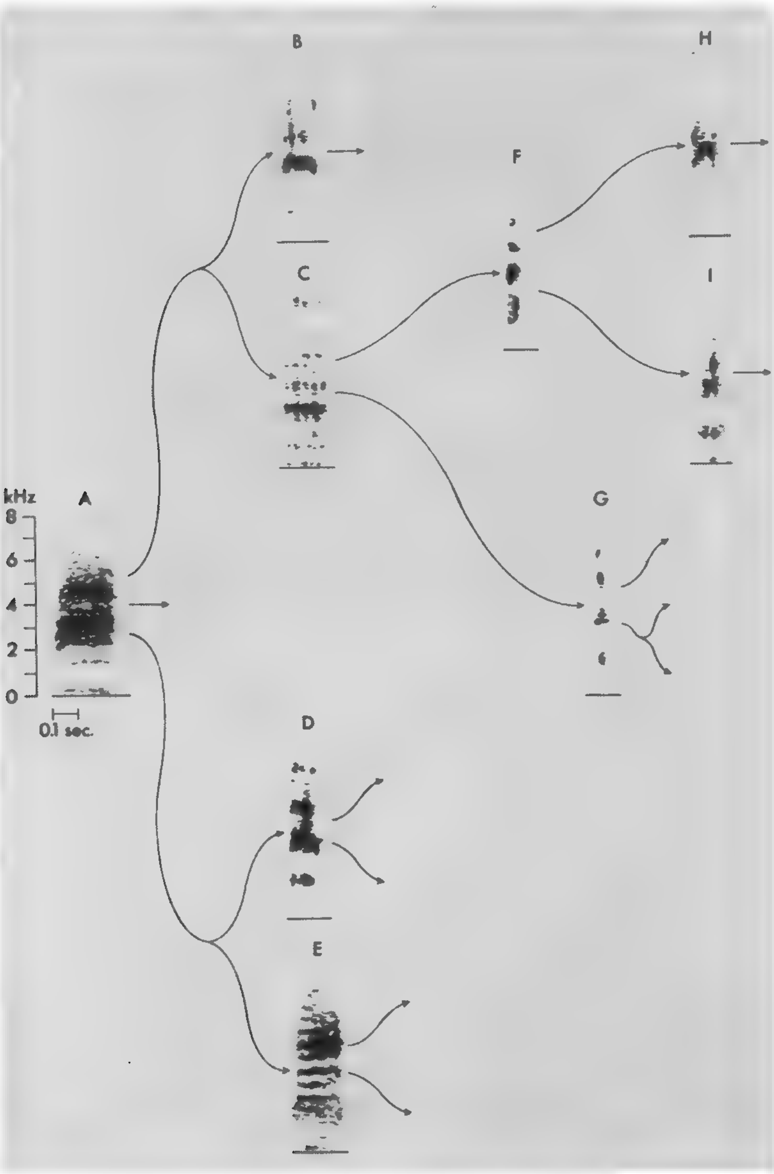

Figure 3. Variation in note structure of adult Northern Jacanas. The notes shown are selected from each of the major continua.

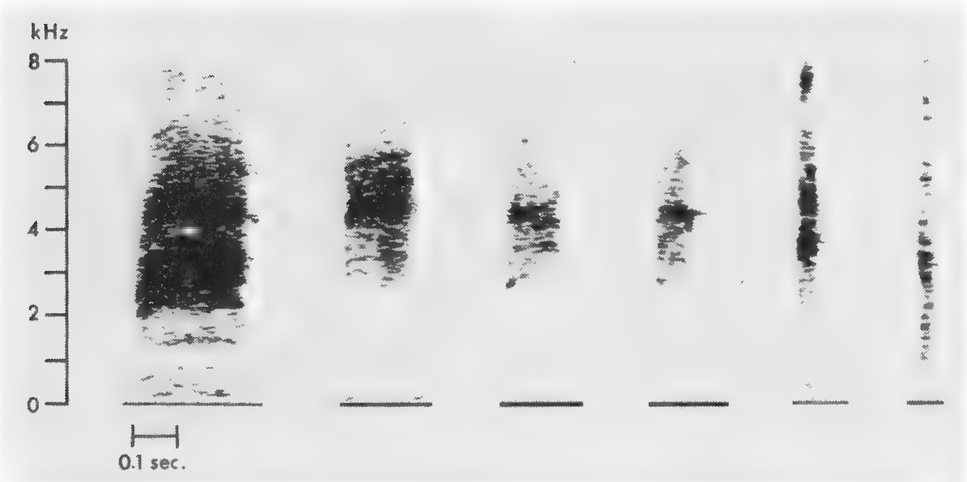

Figure 4. Continuum A showing variation in length of the relatively unstructured notes.

other mainly in whether the high or low frequency bands are emphasized. Notes with emphasis on low bands tend to have more harmonics or spectral bands than notes with emphasis on higher frequency bands (compare upper and lower rows, Figure 6). The length of notes along these two continua varies considerably, but none of the notes appear to be as short as some of those in continua derived from pulsed notes (Figure 5). Notes with numerous conspicuous harmonics or spectral bands fall into two subgroups (Figure 7). The introductory part of the note may consist of a rising frequency modulation, which then flattens (Figure 7, upper row). Alternatively, the bands may appear flat during the first part of the note, and then decline sharply during the last half of the note (Figure 7, lower row).

In addition to these variations of the basic note, there remain a large number of notes, mostly shorter or simpler, that appear to form continua extending from the amplitude-modulated continuum (Figure 3C). Our rationale for starting these continua from the pulsed-note continuum rather than the basic-note continuum is that at least some of the notes are composed of two distinct pulses.

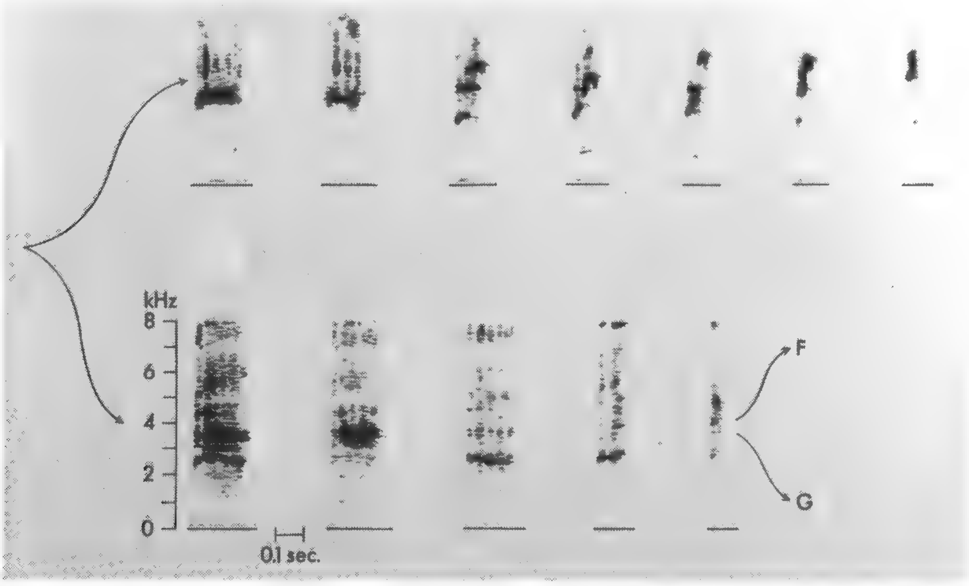

Figure 5. Continua B (*upper row*) and C (*lower row*) show distinct pulsing.

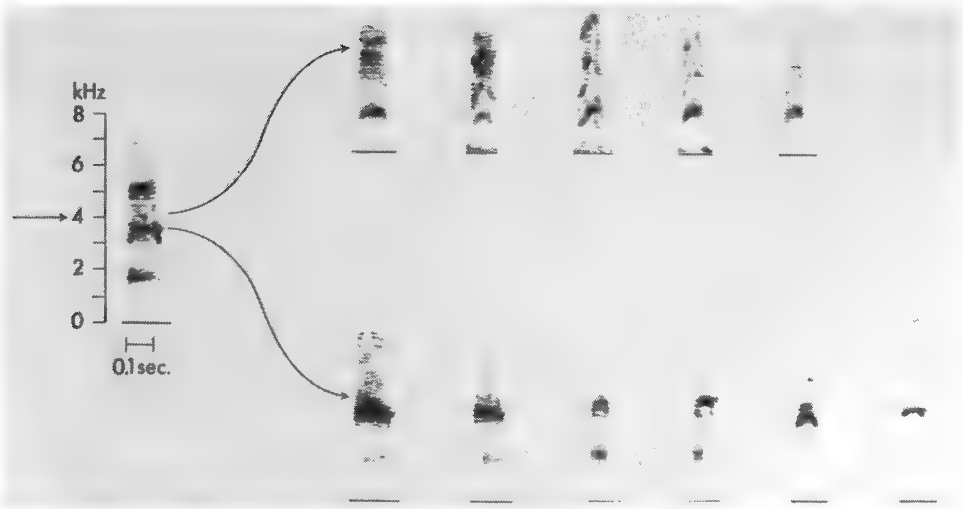

Figure 6. Continuum D. Notes with four or fewer bands may emphasize low or high energy bands (*upper and lower rows, respectively*).

One series of notes appears to be modified from two pulsed notes, which become compressed in time and joined in the region of dominant frequency by a rapidly modulated frequency band (Figures 3F, 3H, 3G, and 8). These notes appear to be further modified by an increased emphasis on the modulated-frequency zone. This occurs by a de-emphasis of the other frequencies and an increase in the duration of the note (Figure 8, left row). Such notes, in which the lower frequencies disappear, may be further modified by pronounced frequency modulation and fragmentation of the dominant-frequency zone (Figure 8, upper rows). Notes of this last type were heard only when the bird was airborne. Another variation of the compressed, double-pulsed note is an emphasis on wide frequency modulation of both parts of the note and the failure of the two notes to merge into a single, relatively narrow zone of dominant frequencies (Figure 8, lower row).

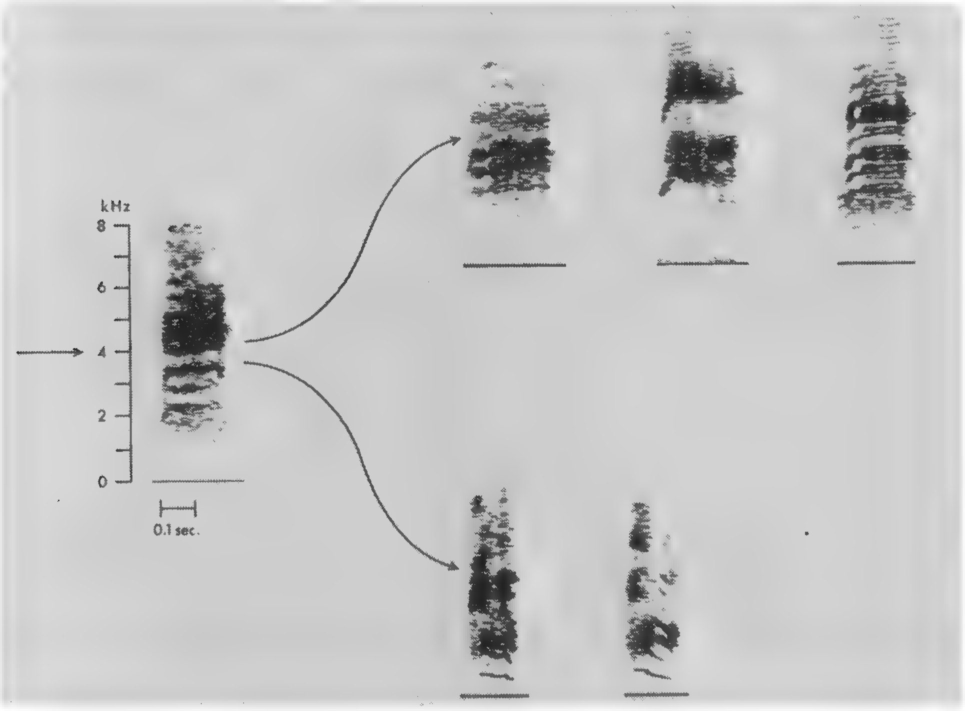

Figure 7. Continuum E. Notes with many bands may increase in frequency in the first part of the note (*upper line*) or decrease in frequency during the note (*lower line*).

The simplest short variation appears to be a concentration of the energy into four zones (Figure 3G and Figure 9, first two notes). These zones may be further reduced in number and the remaining zones variously emphasized. One or both of the high-frequency zones may be emphasized while the lower zones are de-emphasized or missing (Figure 9, upper row). Middle-frequency zones may be emphasized and both the lowest and highest zones lost (Figure 9, middle row). Finally, the highest frequency zones can be de-emphasized or missing and the middle and low zones retained (Figure 9, bottom row). Within each of these continua, there also appears to be considerable drift in the frequency.

Temporal Patterning of Adult Calls

The temporal patterning of the calls of Northern Jacanas varies greatly. At first we felt we could divide the calls into three more or less distinct temporal categories: single- or widely-spaced-note calls, rapidly-repeated-note calls, and clustered-note calls. The clustered-note calls do, indeed, form a unique temporal type. However, the distinction between single- or widely-spaced-note calls and rapidly-repeated-note calls is purely arbitrary, but they do represent the two extremes of patterning in calls other than the clustered-note calls. As descriptive terms, they are useful, but they do not coincide with discrete categories.

Clustered-note calls. — Notes may be clustered in groups of two to four (rarely five) evenly spaced notes. The intervals between the clusters are about double the inter-note intervals within the clusters. At least three variables influence the duration of individual clusters: (1) the number of notes; (2) the duration of individual notes; and (3) the duration of inter-note intervals. Within any one call, the pauses between the clusters are much more regular than are the durations of the clusters. The conspicuous temporal regularity within the call is primarily a consequence of the regular intracluster-intervals.

Temporally variable calls. — The shortest calls consist of a single note temporally isolated from other calls. Other short calls include a variable, but small, number of notes with relatively long intervals between notes. The temporal patterning may be regular or somewhat irregular (Figure 10). Longer calls may begin with introductory phases of the type just described, leading either abruptly or gradually into more rapidly repeated note phases.

The most frequently heard jacana calls are those in which 10 to 45 short notes are given with relatively short intervals between them. These short intervals vary between calls, but are relatively constant through at least the middle portion of any one call. The calls sometimes begin with an acceleration phase in which three or more notes are given with increasingly shorter inter-note intervals. They may also end with a deceleration phase, in which the interval between the last two or more notes gradually increases. Deceleration phases are shorter in duration than acceleration phases. Either, or both, phases may be included, but the regularly repeated notes of the middle phase make up the largest portion of these calls and is the only phase that is invariably present. An interesting variant of this type that we have recorded only a few times is a pattern in which there is a period of silence in place of every third note. This produces a peculiar doublet effect.

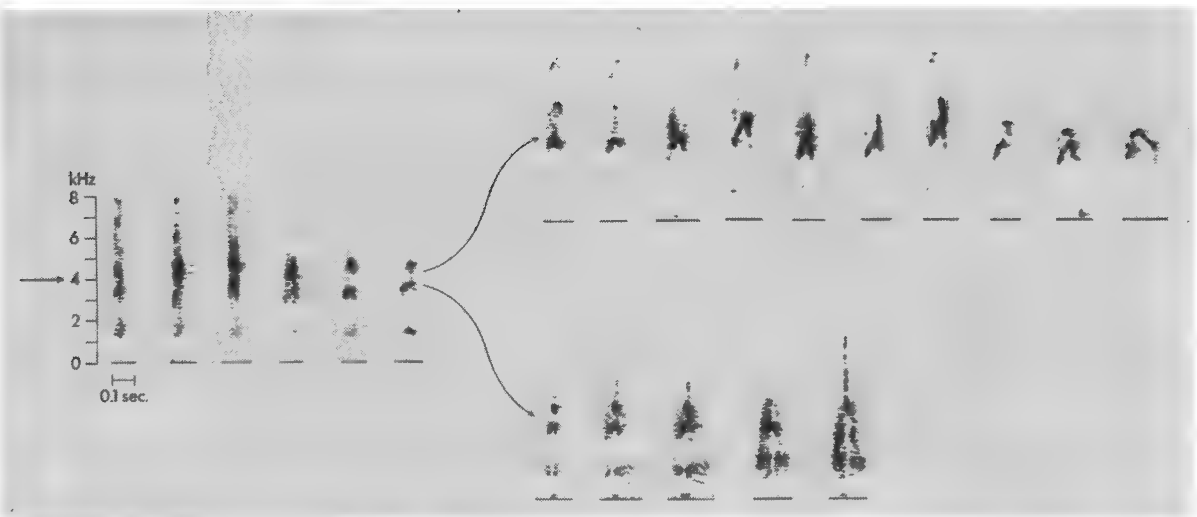

Figure 8. Continua F, H, and I (*left, upper, and lower rows, respectively*). These notes retain and modify the pulsed quality of continuum C.

Relationship Between Temporal Patterning and Note Structure

Single-note calls are most often longer notes from continua A, B, C, D, or E (Figures 4–7), and such notes are almost invariably restricted to calls with single or widely spaced notes. However, we find almost every variation in sonograms of calls with widely spaced notes. Our failure to find some of the shortest notes in these calls may be due to sample bias or size. Widely-spaced-note calls often precede, or lead directly into, calls with rapidly repeated notes.

Rapidly-repeated-note calls include any of the notes from continua F-I (Figures 8 and 9) and the shorter notes from any of the other continua. Although our sample of calls given in flight is smaller than our sample given from the substrate, it appears that any note may be used when rapidly repeated notes are given in flight.

Considerable variation often shows up in the type of note used in repeated-note calls. The structure of the notes sometimes appears to change gradually; at other times, the type of note shifts more suddenly (Figure 11, upper and middle sonograms).

The least variation in types of notes found within calls occurred in calls with the most rapidly repeated notes (Figure 11, lower sonogram). The notes are short; all appear to belong to continuum G (Figure 9), but may bear strong resemblance to other short notes. The rapidly repeated notes used in these calls usually have either wide frequency-range or an emphasis on several frequency zones.

The sonograms of calls given during Flutter Hop displays suggest that mechanical limitations may be imposed on the vocal system by the slow, deeply exaggerated wing beats used in the display. Notes from continuum H (Figure 8, upper line) are the notes most commonly given during Flutter Hop displays.

Clustered-note calls incorporate very short notes. This vocalization is never very loud and on most of our recordings the sound trace is faint compared with that of other calls. For this reason, we may be seeing only the dominant frequency range on some of our sonograms. Other, especially higher, frequency zones may be present.

Intra- Versus Inter-individual Variation

The very large amount of intra-individual variation makes a careful analysis of inter-individual variation difficult at best. Variation in the distribution of sound energy is so complex that any quantitative analysis of it would probably be overwhelmingly complicated. Furthermore, although temporal properties of individual notes would be easier to measure and analyze, we have no reason to believe that they are any more or less important than other variables.

We calculated the range and mid-point of the dominant frequencies and prominent harmonics, note duration, and intervals between notes for a large sample of calls from several individuals. Preliminary analysis of these data support our subjective impression that it will be extremely difficult to bring meaningful quantitative order to the variation. A significant aspect of the problem is the difficulty of obtaining unbiased samples of the vocalizations; we will return to this problem in the Discussion.

Extreme individuality occurred in one jacana recorded in 1972. An unmarked male, later captured and banded, but easily identified because he lacked two toes on his right foot, held a territory along the northeast edge of the lake. Because his vocalizations sounded unique, we made a large number of recordings of his calls. The structure of a large proportion of the notes incorporated in his calls lacked harmonics or spectral banding. Many of his rapidly repeated calls consisted of notes that resembled chick vocalizations in structure but were of lower frequency. Other adults rarely produced notes of this type. This unusual male also frequently used the otherwise uncommon temporal pattern of skipping every third note. Whether this male was an aberrant individual, or whether such unique vocal sets are of regular occurrence, is still an open question.

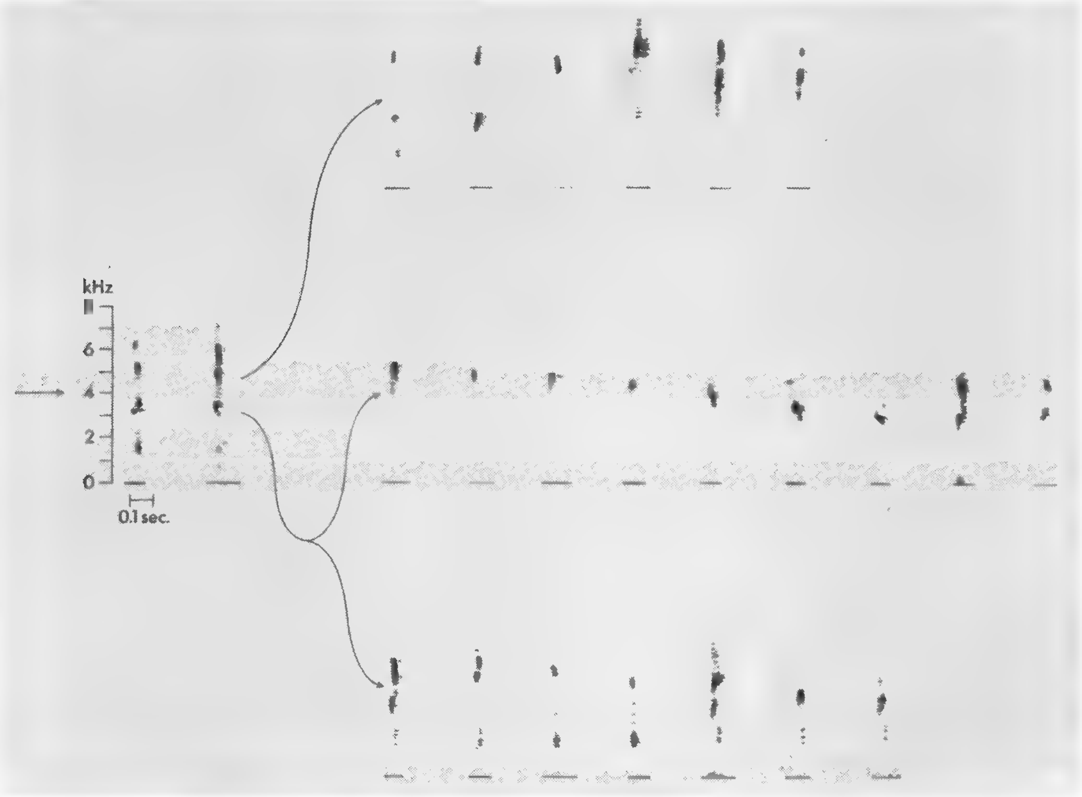

Figure 9. Continuum G contains short notes in which the energy is concentrated in four zones that may be emphasized differentially.

Discussion

We hypothesize that the vocal repertoire of adult Northern Jacanas consists of only two different calls. One, the clustered-note call, is relatively stereotyped and characterized by a unique temporal patterning of clusters of individual notes. The notes are always very short in duration. All of the other vocalizations we studied appear to belong to a graded system in which the number of notes, details of note structure, and the temporal patterning of the notes are all highly variable, and in which little, if any, ritualization or stereotypy occurs. Although variation in this system is great enough to allow for the encoding of a wide variety of specific messages, we do not have any evidence that this happens. The clustered-note call corresponds to the Chickety Call of our subjective classification; but the five other subjectively identified calls are only aurally conspicuous variants and are not really separable.

The vocal communication system of adult Northern Jacanas may be functionally very simple. Clustered-note calls, although used in a variety of contexts, occur only between mated birds and occasionally between a male and his chicks. In aggressive interactions between a pair and one or more jacanas, the clustered-note calls sometimes may be heard — probably between the mated birds. Adult jacanas render all other vocalizations under two different circumstances. First, in response to some apparent threat by a predator to the adults, their nest, eggs, or young; second, in response to territorial intrusion by one or more conspecifics. The particular note or notes used and the temporal patterning of those notes could be a reflection of the apparent urgency of the situation. Such a vocal system would serve to alert the male, orient it, and convey some measure of the seriousness of the threat. The potential recipient may ignore the signal; or it may stop its ongoing behavior and look toward its vocalizing mate, then go to the mate, or return to its previous behavior; or it may immediately fly to its mate, apparently without any preliminary visual orientation. Jacanas are diurnal, and once altered and oriented, the second bird may be able to visually identify the danger.

Because conspicuous differences are not evident between the calls given before the mate arrives and those subsequently produced by both birds, the calls probably serve additional functions. They may continue to function as contact communication between members of the pair, and/or as threat signals directed at intruding conspecifics or predators. If it is true that calls represent a graded system, intruders should be able to determine the degree to which territorial birds react to their presence. Although such interactions may include chasing and fleeing, they seldom lead to direct physical attacks.

Volume, duration, and repetition-rate of the notes may be the important variables in these calls. Note structure may not be important in itself, but may be a consequence of loudness, duration, and repetition and, therefore, may provide a degree of redundancy. The duration of notes often appears to be inversely related to repetition-rate.

Temporal qualities of the vocalizations of the Northern Jacana vary greatly in two obvious and independent parameters: length of individual notes and their patterning. Calls may contain single notes; repeated notes spaced widely and evenly, or unevenly; rapidly repeated notes with, or without, accelerated introductions and decelerated endings; or clustered

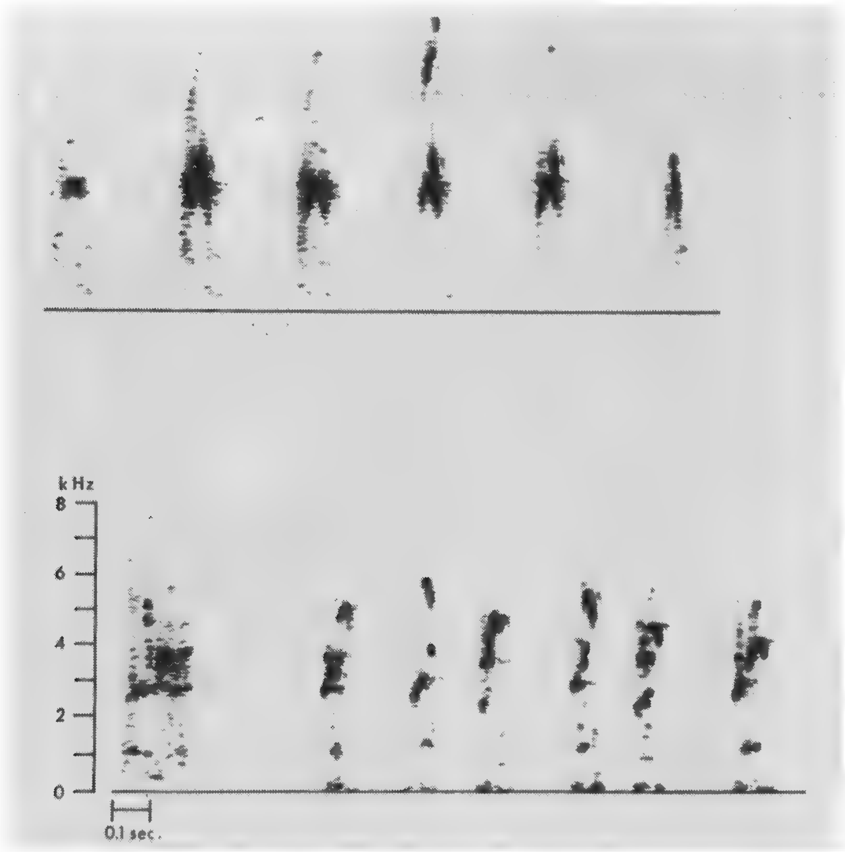

Figure 10. Sonograms of widely-spaced-note calls with regular cadence and irregular cadence.

notes with greater intervals between the clusters than between the notes within the clusters. All of the calls with repeated notes may vary in number of notes, in length of inter-note interval, and in constancy of the interval. Less obvious perhaps, and not completely independent of note duration, are various temporal properties within individual notes. Variations of this sort include the number and duration of pulses, and duration of ascending, descending, or unchanging frequencies.

Males occasionally give repeated-note calls in the absence of any threat, while standing alone on the copulation site. In this context, the vocalizations apparently function to attract the female. One monogamous male gave such calls throughout the afternoon of the day on which his female was killed by a car during a mid-morning rainstorm. Neither predators nor conspecifics were present in his territory.

All of our recordings of the last two notes of the lower line of continuum E (Figure 8) are of birds calling at a slow repetition-rate in response to the presence of turtles that posed no immediate or serious threat. Other notes also are used in response to turtles.

Jacanas use the clustered-note calls when communicating over relatively short distances. They render these calls in varying contexts: when the male is alone and undisturbed in his territory and the female has been away for some time; preceding and during copulation; while standing over the eggs or incubating; when one chick becomes separated from the male; and occasionally during extended territorial fights, when the partner is also present. As in all jacana vocalizations, visual communication usually accompanies the vocal behavior. The call apparently serves to reduce the distance between the two birds or keep them together.

We are convinced that the repertoire of notes in the vocalizations of the Northern Jacana is a graded system. If the vocal system is composed of specific syllables, they must be either extremely numerous or highly variable. A critical question that remains unanswered is how much stereotypy, or typical intensity, exists in the system. If we made a frequency distribution of the different note types, we suspect that we might find modal peaks on such a distribution that would allow us to identify and describe typical intensity note-types (Morris, 1957). However, for a frequency distribution to be of value, it should be based on a large and unbiased representative sample of jacana vocalizations. Our sample is biased toward vocalizations that are loud, accompany conspicuous visual displays, occur in response to conspicuous external stimuli, and probably in other ways not readily apparent. We could avoid much, but not all, of this bias by a fixed interval sampling technique. However, some of the sounds are produced at very low intensities; the territories, especially the female territories, are relatively large (Jenni and Collier, 1972); and several birds often vocalize more or less simultaneously. Dividing the continuum into discrete note-types on the basis of a frequency-distribution would require constant differences between adjacent notes. However, variations in the structure of the notes might not parallel differences in their meanings, the factors responsible for their production, or the functions of the notes. This, of course, is the dilemma we would like to resolve.

Most of the research on variation in vocal systems has been done with songbirds. In this group, songs and individual syllables are relatively conspicuous and suitable for analysis. Some of the more elegant studies have covered such diverse aspects as geographic variation, patterning or sequencing of syllables within songs, species specificity, inter- and intraindividual variation and recognition (Bertram, 1970; Emlen, 1972; Lemon and Chatfield, 1973; Marler and Issac, 1961; Smith, 1970). Although relatively few researchers have studied natural variation in the vocalizations of non-passerines, several workers demonstrated that adults of various colonial-nesting birds produce individually distinct calls (Beer, 1970; Jouventin, 1972). Recently, a few descriptive studies of the vocal repertoires of non-passerines have appeared (Heinz and Gysel, 1970; Martin, 1973; Ridpath, 1972; Storer, 1969). In addition to short descriptive papers on vocal behavior of other Charadrii, there are a few extensive analyses. Oring (1968) recognized two song types and five calls in both Green and Solitary Sandpipers (*Tringa ochropus* and *T. solitarius*). Oring mentions the possibility that at least some of the calls might belong to a graded system. Forsythe (1970) correlates the functionally depauperate vocal repertoire of the Long-billed Curlew (*Numenius americanus*) with the open habitat of the nesting birds and the apparent heavy reliance of these birds on visual signals. Bursian (1971), in a study of variation in Killdeer (*Charadrius vociferus*) vocalizations, found one distinct type of vocalization that accompanied a broken-wing display. All other calls appeared to belong to a continually graded system that could be subdivided into natural sub-units. Apparently, vocal systems in the Charadrii range from highly stereotyped to highly variable.

Surprisingly, the descriptions and sonograms of the graded vocal systems of some primates (Marler, 1972) bear stronger resemblance to the system we find in the Northern Jacana than do studies of other avian systems.

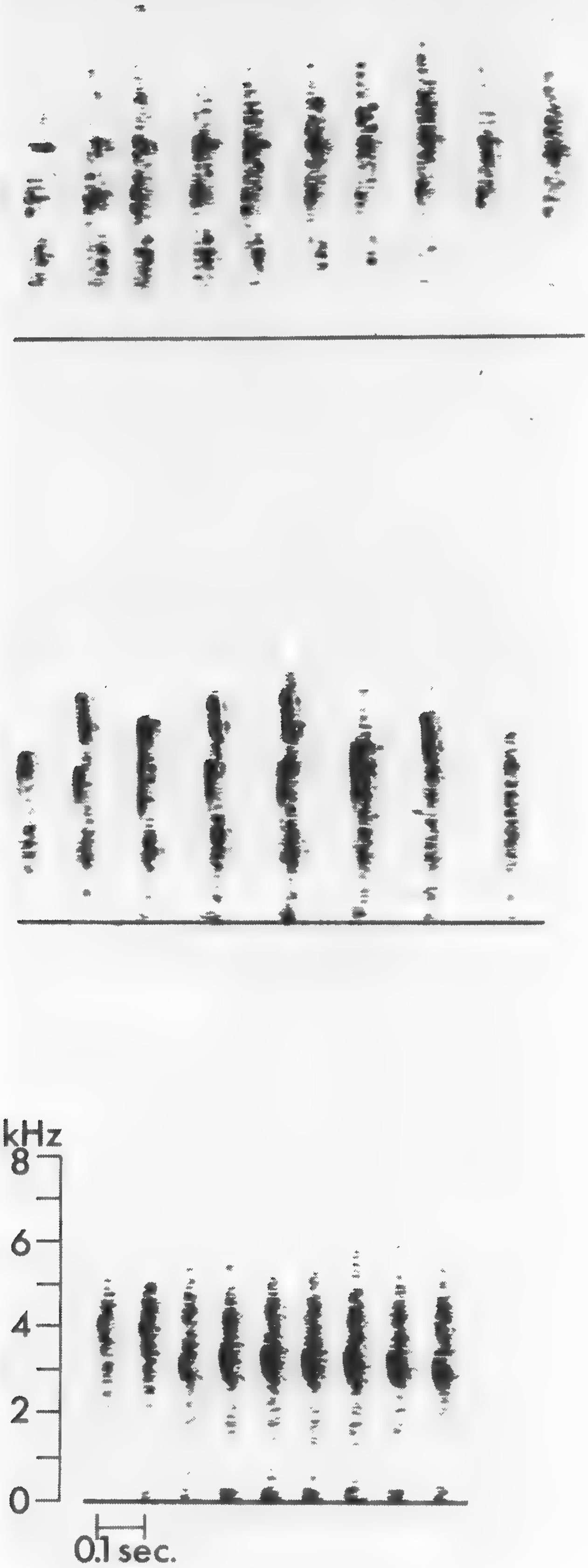

Figure 11. Sonograms of rapidly-repeated-note calls, showing gradual changes in note types *(upper)*, sudden changes in note types *(middle)*, and very short inter-note intervals *(lower)*.

However, these primate systems appear to be more complex and include a relatively large number of different, although highly variable, vocal signals.

This attempt to order and describe the vocal behavior of the Northern Jacana raises many questions, some of which are quite general and apply to any analysis of avian vocalization. The most critical problems relate to sampling methods and subjective evaluations. It is easy to classify the sounds subjectively, make recordings of the typical sounds, and analyze them. It is difficult to bring unarbitrary order to the variation.

We have not considered the difference in relative loudness within, and between, calls, but it, too, is a conspicuous variable. The observer, trying to obtain the best quality recording possible, adjusts the record level of his tape recorder up or down according to the manufacturer's instructions. A traditional sonographic analysis tells us little about loudness. Amplitude in sonograms tell us about relative loudness at different frequencies within a note, but does not provide good measures of absolute loudness between notes or calls. We could measure the sound level at the microphone, but distance to the calling bird and its orientation are difficult to measure and often change during calling. We need to develop more precise measuring methods before we can compare quantitative variation in loudness between individual notes and calls.

It will be difficult to test the hypothesis that the vocal system of adult Northern Jacanas consists of only two communication types, one relatively stereotyped and the other graded both in the structure and temporal pattern of notes. The first problem, already discussed above, is that of obtaining a large and unbiased sample of vocalizations. We have also discussed the problems of analyzing such a sample without imposing artificial constraints. The analysis is fraught with opportunities for circularity and other errors of judgment. Although we work in an age of sophisticated computer analysis, humans still program the computer.

It will be necessary to analyze the calls functionally. We can record the behavioral context in which the calls are given and the consequences that follow each vocalization. However, no two contexts are identical, nor are the subsequent responses. They can be classified into discrete categories; but such a classification must be partly artificial and seems inconsistent with the apparent graded nature of the vocal system. However, no other approach appears reasonable to us. If we find modal peaks in unbiased frequency-distributions of note-types and/or temporal-types, we would expect to find parallel modal peaks in the causal factors and functions of the calls as well.

We keep returning to our initial, albeit subjective, analysis and asking, "Is this correct and the rest of the analysis much ado over nothing?" Unfortunately, we cannot convince ourselves that perhaps the truth lies with the simpler analysis. If we had been more discriminating in our recording and recorded only the most typical calls, or more critical in the selection of recordings for analysis, or both, we might have been able to believe that the subjective description was correct. The basic dilemma is that early subjective impressions easily could lead us, and perhaps other workers as well, to the collection of typical vocalizations (that is, those that correspond to our subjective categories), and the subsequent analysis of variation which, although having all the appearances of scientific respectability, would center about norms that have not been objectively identified.

Summary

The vocalizations of breeding Northern Jacanas can be subjectively divided into six adult call-types and one vocalization by chicks. Sonographic analysis of large numbers of adult vocalizations shows that five of these six classes appear to belong to a single graded system. The two most conspicuous variables are the details of note structure and temporal patterning. Individual notes vary from relatively long, unstructured notes to types which (1) emphasize either pulsing or frequency modulation, (2) have complex internal structure, and (3) are very short in duration with great variation in emphasis of frequency. One temporal pattern, the clustered-note call, is relatively stereotyped and composed of very short notes. This call appears exclusively between mated birds and males and their young. The remaining calls contain a highly variable number of notes that differ widely in details of note structure and intervals between notes. They are produced in response to potential predators or territorial intrusion by conspecifics. If the mate is absent, they apparently serve to attract him or her to the territory. Both birds, when present, call, and the vocalizations must serve as a signal between the pair and/or as a threat to predators or intruding conspecifics.

It is our impression that repetition-rate of the notes within the call is the most important variable. Less so, perhaps, is note structure, at least in calls with more rapidly repeated notes. Perhaps variation in structure is actually a consequence of repetition-rate and of volume, which may also be an important variable, although we have been unable to measure it objectively.

Acknowledgments

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THE EVOLUTION OF CLUTCH SIZE AND MALE "CHAUVINISM" IN THE WHITE-BEARDED MANAKIN

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Monogamy is the most widespread and probably the most primitive type of heterosexual affiliation among birds (Lack, 1968). Assuming that avian reproductive rates have evolved under the influence of natural selection, total liberation of one sex from a parental role will have occurred where the other can rear more young than the pair together. It will also occur, if one sex can rear as many young as the pair and the liberated sex can increase its reproductive rate through emancipation. Among birds, the greater incidence of liberation of males from parental care of eggs and young presumably relates in part to the fact that the male produces larger numbers of gametes with a much lower energy expenditure and, thus, usually has an infinitely greater capacity to increase his reproductive rate through polygamy. Also, the male's parental role in monogamous species more commonly is smaller and of a more indirect nature than that of the female. Liberation of one sex from a parental role is more common in nidifugous species (the young leave the nest soon after hatching) than in nidicolous species (the young remain in the nest for an extended period after hatching); the former are more independent at hatching and so the parental work load is more frequently reduced to a level at which it can be borne by one sex.

The White-bearded Manakin (*Manacus manacus*) is one of several known lek-forming species in the family Pipridae. This manakin is strongly dimorphic sexually and the promiscuous black and white males display in groups of 6 to 60 throughout the year (except during molt) at traditional forest-floor arenas (Lill, 1974a). As in other lek birds so far studied, the female alone builds the nest and rears the young. The clutch consists of two, or occasionally one, proportionately large eggs. The period of nesting is similar to that of many passerines of the same size and generally similar ecology, but manakins incubate for an unusually long period relative to the duration of the nestling phase (Lack, 1968). The female feeds the fledged young but the period of dependency is unknown. Reproductive success is poor due to very heavy nest predation (Snow, 1962a), but annual survival is high, both sexes being extremely long-lived (Lill, in press, b; Snow and Lill, 1974).

The Problem

Snow (1962a) argued that the small clutch size of *M. manacus* was an important factor in the evolution of male liberation from parental care. He agreed with Skutch (1949) that the small clutch typical of many open-nest birds of neotropical forests evolved in response to heavy nest predation. Such predation confers a selective advantage on nests that need visiting seldom and are inconspicuous. Snow suggested that the abundance of fruits on which the female feeds enables her to satisfy her food requirements and those of her small brood rapidly and without male assistance, and, further, that heavy nest predation would strongly promote male liberation if the male was more conspicuous than the female. However, Lack (1966) pointed out that nest predation in the manakin was equally heavy during the incubation and nestling stages, although the rate of nest visitations was four times greater during the latter stage. He argued that predators find nests ". . . by looking in likely places," not by observing the visits of parent birds. Lack suggested that insects probably comprised a more important component of the nestling diet of *M. manacus* than Snow's observations indicated, and proposed that the brood size was limited by the availability of insect food for the nestlings.

Identifying the factors limiting the clutch size of manakins is thus germane to understanding the evolution of male liberation and polygamy in this family, as well as the important and more general problem of why tropical birds tend to have lower reproductive rates and clutch sizes than temperate species. Skutch (1949, 1967) rejected Lack's (1947, 1948, 1966) concept of a "maximized" reproductive rate for tropical birds living in stable environments in favor of a reproductive rate adjusted to low adult mortality through group selection. He also argued against Lack's idea that the clutch size of tropical, nidocolous species was determined by food availability for the young, pointing out the similarity in clutch size of polygamous species like the manakins and certain flycatchers in which one sex cares for the young, and some cohabiting monogamous species in which both sexes have a parental role.

In this paper, I review observations that result from field experiments and theoretical arguments concerning the factors limiting clutch size and promoting unisexual brood-care in the White-beared Manakin. It seems likely that many of the arguments presented here may apply equally well to other species in the genera *Manacus* and *Pipra*, whose breeding biology is very similar (Skutch, 1960; Lill, 1974c).

Study Area and Methods

I observed the White-bearded Manakin in the lower Arima Valley of Trinidad (10–11° N Lat., 61–62° W Long) from 1967 through 1971. The natural vegetation of the area is transitional between montane rain forest and deciduous seasonal forest, but has suffered some disturbance through localized cultivation. Beebe (1952) and Snow (1962a) provide detailed descriptions of the ecology and climate of the area. There is one wet season (June–December) and one main dry season. And in most years, the main breeding season of *M. manacus* overlaps the two, with a peak occurring early in the wet season. The White-bearded Manakin and the Golden-headed Manakin (*Pipra erythrocephala*), which is the only other manakin occurring in Trinidad, are two of the commonest members of the forest avifauna.

I found some *M. manacus* nests in all five years, but most of the observations reported here I made from March through July in 1968 and 1971, when regular nest searches were carried out at five- or seven-day intervals. Weights (to the nearest 0.5 gram) of eggs and nestlings were obtained with a Pesola spring balance. I assessed the diet of nestlings from the contents of dissected stomachs. I experimentally increased the normal brood size by adding a third nestling of comparable age and weight to a brood of two as soon as possible after the hatching of the second chick.

Factors Influencing Clutch Size and Unisexual Brood Care

Availability of Food for Nestlings

To apply Lack's (1966) thesis that availability of insect food for the nestlings limits brood size in *M. manacus,* we must demonstrate (1) that insects compose a significant percentage of the nestlings' diet, and (2) that the nesting female cannot, as a rule, adequately feed more than the usual two nestlings.

I analyzed the stomach and anterior gut contents of seven nestlings of various ages and from different locations within the 450-acre study area. Three specimens were collected in March and four in June 1971. Facilities were not available at the time for accurate measurement of the very small volume of gut contents, and so I made, as objectively as possible, a visual estimate of the fruit-to-insect ratio of the remains (Table 1). Insect material composed from one-fourth to three-fourths of the gut contents of all specimens, the mean gut content index (fruits/insects) being 1.4. No age or locational trends in the relative representation of fruit and insect remains were apparent in this limited sample. Although the sample was small and the measurement relatively unsophisticated, it is clear that insects composed

TABLE 1

Gut Contents of Seven *M. manacus* Nestlings of Varying Ages, Trinidad, 1971[1]

Index of gut contents (fruit/arthropods)	*Brood size*	*Estimated age (days pre-fledging)*	*Nest location*	*Nestling weight (gms)*
2	2	5–1	TB	11.0
.5	1	7–1	J	10.0
2	2	8–7	J	8.5
1	2	11–10	J	6.5
.333	2	11–10	TB	5.5
1	2	14–13	AR	3.0
3	2	14–13	TB	3.0

[1] After dissection, ratio of fruit to arthropod material was estimated visually to the nearest one-third or one-fourth of contents. All guts contained both food types. Stomach and fore-gut contents were analyzed. In making age estimations in comparison with undisturbed broods, the day when all, or the first nestling, fledged was called Day 1. Nest locations are: TB = Tripp Branch stream, J = Jumbie stream, and AR = Arima River. They are shown in Snow (1962a) and Lill (1974b).

a significant proportion of the nestling diet of *M. manacus* in the study area in 1971. Potentially, therefore, insect availability could influence brood size.

Ability of Females to Rear More Than Two Young

I attempted to determine whether females could adequately feed and rear more than the usual number of nestlings. I supplemented each of six broods of two young with an additional chick of comparable age and weight as soon as possible after the second nestling hatched, usually on the same day. I weighed all nestlings at the time I increased the brood size and at regular intervals thereafter. They were not individually marked, however, so the foster nestling could not be identified after the transfer. Growth rate in experimental broods (three nestlings) was compared with that in 11 normal broods used as controls. The high nest predation rate on *M. manacus* in the study area limited the size of this experiment. Both categories comprised broods with a range of hatching dates covering most months of the 1971 breeding season.

At ages when weights of normal sized broods were not available for comparison with the weights in some enlarged broods, I have quoted predicted control values derived from regression equations. These are only estimates, and the magnitude of the sampling error inherent in their computation, even with large samples, is such that potentially biologically significant weight differences on the order of one to two grams will not be detected. However, in the instances where predicted control weights have been cited, comparison of the growth curves of nestlings in supplemented and control broods, and of supplemented brood nestling weights with the weights of control nestlings of the nearest comparable age, removed any ambiguity about the observed similarities and differences in growth rate.

Figures 1, 2, and 3 compare growth rates of normal broods comprised of one nestling, two nestlings hatched synchronously (on same day), and two nestlings hatched asynchronously (different days). To my knowledge, the growth curve has been documented in only one other manakin species (Lill, 1974c), and for relatively few neotropical frugivores. Inter-brood variability in the hatching interval introduced an empirical, rather than a practical, difficulty in comparing growth rates of experimental and control broods for reasons given later. This was overcome by comparing broods having the same hatching interval. Weight comparisons between members of normal two- (synchronously and asynchronously hatched) and one-chick broods were possible for six stages of nestling development. No significant differences were apparent (for 12 comparisons with d.f. 2–7, $p > 5\%$, t-Test) other than a disparity in the fledging weights of one-chick and asynchronously-hatched two-chick broods ($t_4 = 2.882$, $p < 5\%$, t-Test). However, asynchronously-hatched broods fledged asynchronously and this comparison was for the date when the first nestling fledged. Therefore, the observed statistical difference is misleading and probably of limited biological significance. Nestlings in normal broods of two and one had similar growth rates, and single-chick broods were included in the controls.

Figures 4 through 8 compare the growth rates of supplemented and control broods. Regression coefficients for the experimentally enlarged broods did not differ significantly from those of controls (t-Tests with 8–48 d.f., $p > 5\%$ in all cases). This suggests that supplementation did not significantly depress mean nestling growth rate throughout the subsequent

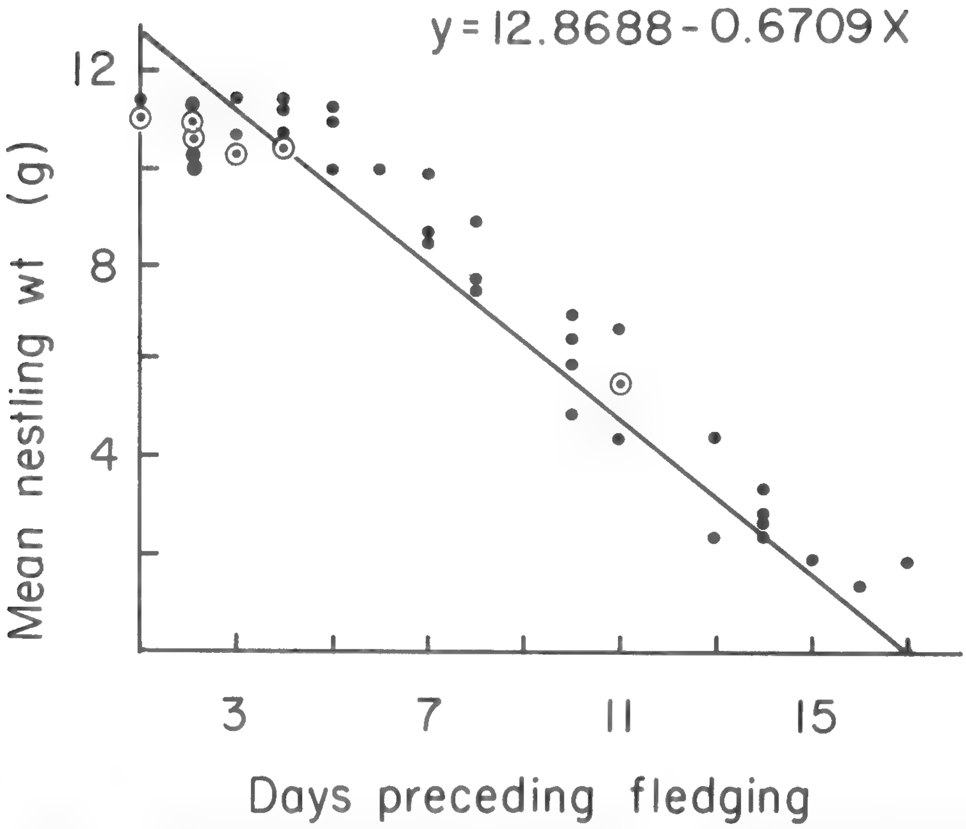


Figure 1. Growth rates of nestlings in undisturbed broods of the White-bearded Manakin in Trinidad, 1971. The diagram shows regression of weight on age for broods with single nestlings and those with two nestlings hatching synchronously. Circled points indicate two identical readings. Regression lines fitted by least-squares method.

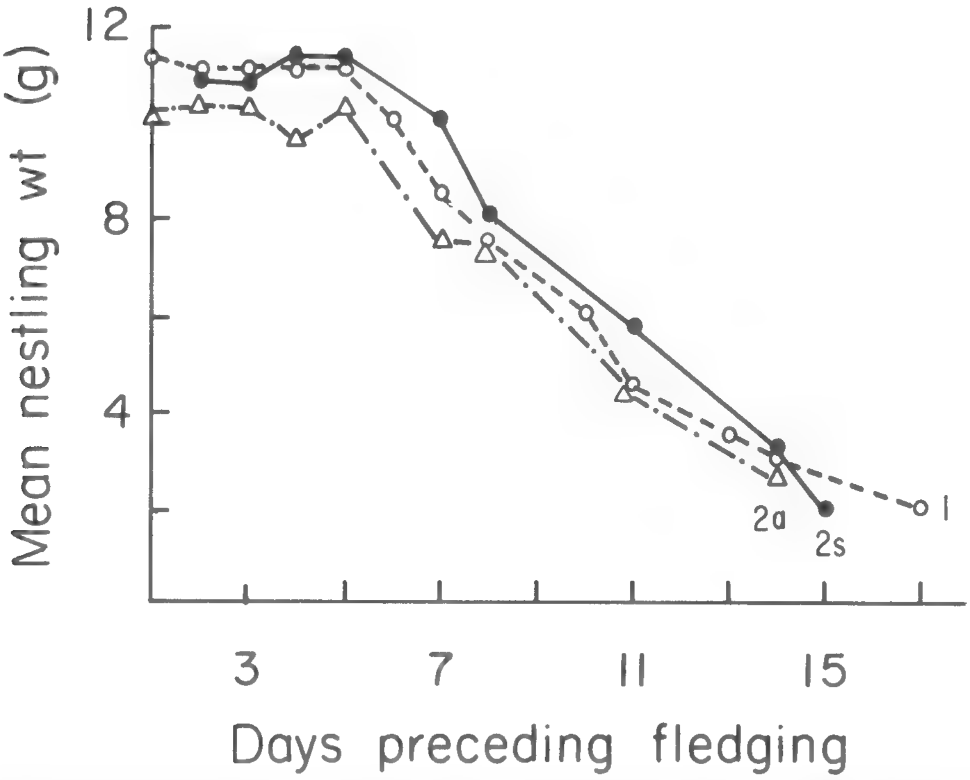


Figure 2. Growth curves for undisturbed broods with single nestlings (1), broods with nestlings hatching synchronously (2s), and broods with nestlings hatching asynchronously (2a). Day 1 equals day of fledging of entire brood or of first chick to leave in an asynchronously hatching brood (2a). Circled points indicate two identical readings.

period of nestling development. It does not exclude the possibility that a significant effect on mean nestling weight may have occurred only near the end of the developmental period or that the growth rate of a single brood-member may have been differentially affected by supplementation.

Supplemented broods SP3M and TB28 showed the two most extreme results. I found the lightest nestling (4 gm) of brood SP3M dead in the nest five days before fledging was due (Figures 4–8). Its gut was empty, and both it and the lighter of the two living nestlings (9 grams) weighed significantly less than the mean weight of controls of the same age ($t_5 = 10.88$, $p < .1\%$ and $t_5 = 2.76$, $p < 5\%$). The dead nestling had been significantly underweight at 11 days pre-fledging and clearly died of starvation. The surviving brood-members fledged on schedule at normal weight. Brood TB28 disappeared 13 days after hatching (or within two days of fledging) apparently because of predation, since the nest-bearing sapling had been broken down (Figures 5 and 8). Comparison of the weights of these broods with the controls was impossible, but mean nestling weight began to drop well below the predicted control value between six and nine days after hatching. When the brood was last weighed 12 days after hatching, the mean nestling weight of 8.5 grams was 1 to 2 grams below the predicted control mean and clearly significantly lower than in supplemented broods of closely comparable age (see Figures 1–5). The three nestlings weighed 8, 9, and 9.5 grams, the lightest being 1.3 to 2.7 grams lighter than the predicted control mean nestling weight. Both lighter nestlings were considerably underweight for their age, since nestlings in undisturbed broods weighed at least 10 grams at about this age (Figures 1–3). These birds appeared healthy, however, and with normal feathering for their age. I think they would have fledged if they had not been depredated, but it seems likely that the survival potential of the lighter nestlings would have been impaired.

Supplemented brood 21MJ lost two members due to an unknown cause four to five days before fledging when the mean nestling weight of 9.5 grams was significantly less than that of controls ($t_5 = 2.841$, $p < 5\%$); at this time no individual nestling was significantly underweight statistically, but the lightest nestling was two grams lighter than any control of the same age. The depressed mean nestling weight was apparent only shortly before brood reduction and the surviving brood-member fledged on schedule at normal weight.

Brood 6MJ remained intact for at least one-third of the nestling period when the mean nestling weight of 7 grams was only 0.1 to 0.2 grams less than the predicted mean weight of the controls; and the weights of the individual nestlings (6.5, 7, and 7.5 gm) were similar to those of controls of nearly the same age. Between the ninth and fifth days pre-fledging, one chick was lost due to an unknown cause; the two survivors were normal weight for their age.

Brood SP1, supplemented on the day of hatching, survived intact only four days. On day four, when the mean nestling weight of 3.3 grams was 1.5 grams below the predicted control value, and clearly much lower that that noted for controls of a closely comparable age (see Figure 4), I found one nestling alive on the ground below the nest. Whether it had fallen from the somewhat tilted nest or had been evicted by the female was unclear, but the latter seems more likely since, at that age, *Manacus* nestlings are relatively immobile in the nest and do not move to the rim to defecate. I replaced the young bird, but brood reduction from an unknown cause oc-

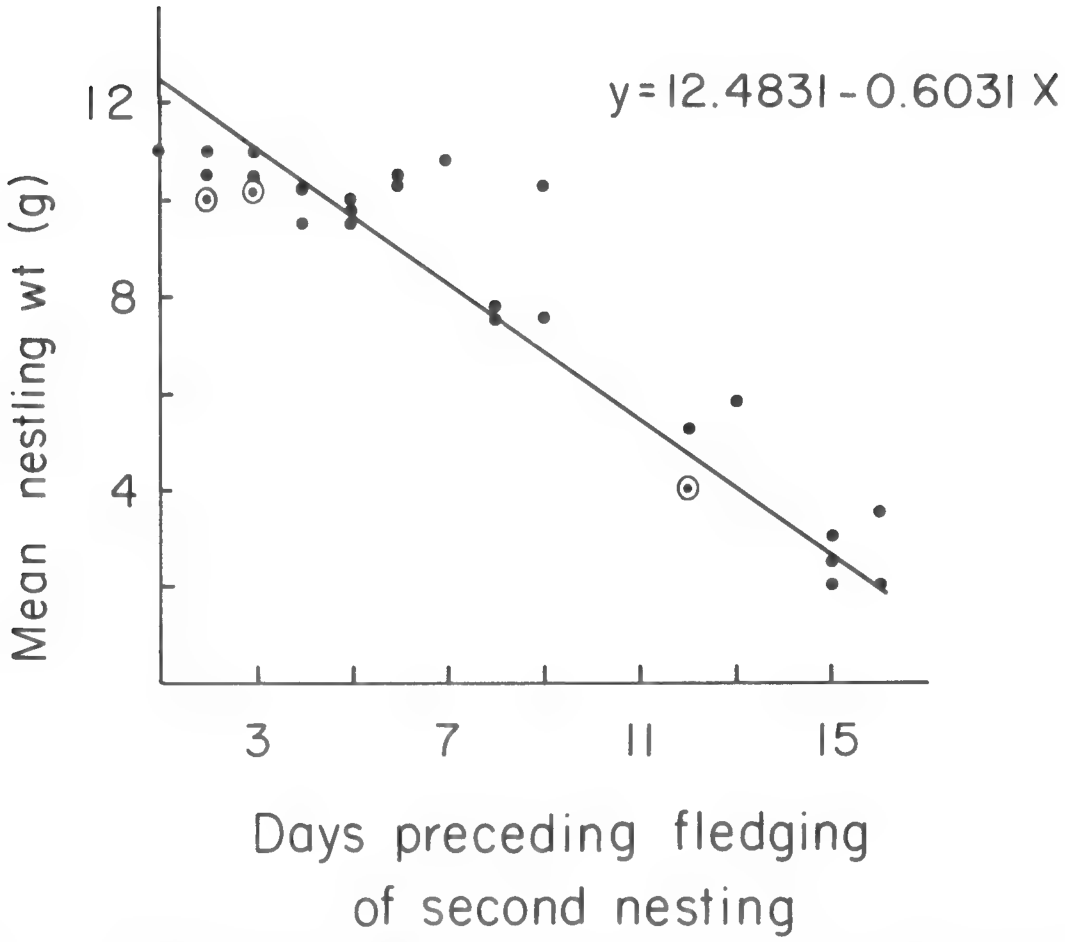


Figure 3. Growth rates of nestlings in undisturbed broods of the White-bearded Manakin in Trinidad, 1971. Diagram shows regression line for weight on age for broods with nestlings hatching asynchronously. Day 1 equals fledging day of second nestling. Circled points indicate two identical readings. Regression lines fitted by least-squares method.

curred two days later. The surviving nestling was probably preyed upon while underweight and overdue in nest departure; either early retardation of its growth slowed down its entire rate of development or the female was for some reason inefficient in her feeding behavior. Supplemented brood AR3 was reduced within the first 24 hours when, for reasons unknown, only one nestling remained in the nest. This nest furnished no useful data on brood size limitation.

The results of this small number of brood size manipulations are not entirely clear-cut because the reasons for the disappearance of nestlings were not certainly known and comparisons of actual nestling weights were not always possible. The female with brood SP3M was clearly unable to feed more than two nestlings adequately. The female of brood TB28 probably could have reared successfully her enlarged brood but one or more members either would have fledged late or fledged on schedule but underweight, and thus have been less likely to survive. Nestling growth rate was significantly reduced in two other artificially enlarged broods (SP1 and 21MJ) but not in a third brood during the first third of the nestling period for which it remained intact. It seems reasonable to conclude that *M. manacus* females in the study area were apparently incapable of adequately feeding a larger than normal brood in 1971 as predicted by Lack's (1966) hypothesis.

Asynchronous Hatching

Snow's (1962a) description of the incubation period in *M. manacus* suggests he may have observed some asynchrony of hatching in this species, but he does not describe its extent or discuss its possible significance. In my investigation, I recorded asynchronous hatching — that is, the chicks hatched on different days — in six of the nine broods for which the hatching date of both nestlings was ascertained. Hatching intervals were one day (two broods) and two days (three broods) for broods in which asynchronous hatching was accurately determined. Snow (1962a) stated that "the female does not usually sit until the second egg is laid." I did not determine when incubation started in asynchronously hatched broods, but it seems likely that it commenced on the day the first egg was laid or on the following day. Skutch (1960) noted that the female sometimes incubates before completing the clutch in the related Orange-collared Manakin (*M. aurantiacus*), which has a very similar breeding biology. However, if this is so, it renders less plausible Lack's (1968) hypothesis that *M. manacus* lays eggs at two-day intervals because of the female's difficulty in getting enough food to form the proportionately large egg; for incubating before the clutch is complete would significantly reduce available foraging time for the laying female.

Lack (1968) argued for the adaptiveness of asynchronous hatching in nidicolous birds when food for the young is sparse, because the younger and less developed nestlings cannot compete effectively with their older siblings for limited food supplies brought by the parents. Thus, food and energy is not wasted on young destined to die anyway and the brood is rapidly reduced to the size which the parents can adequately feed.

The mean weight difference between *M. manacus* brood-members shortly after hatching of the second nestling was not significantly different

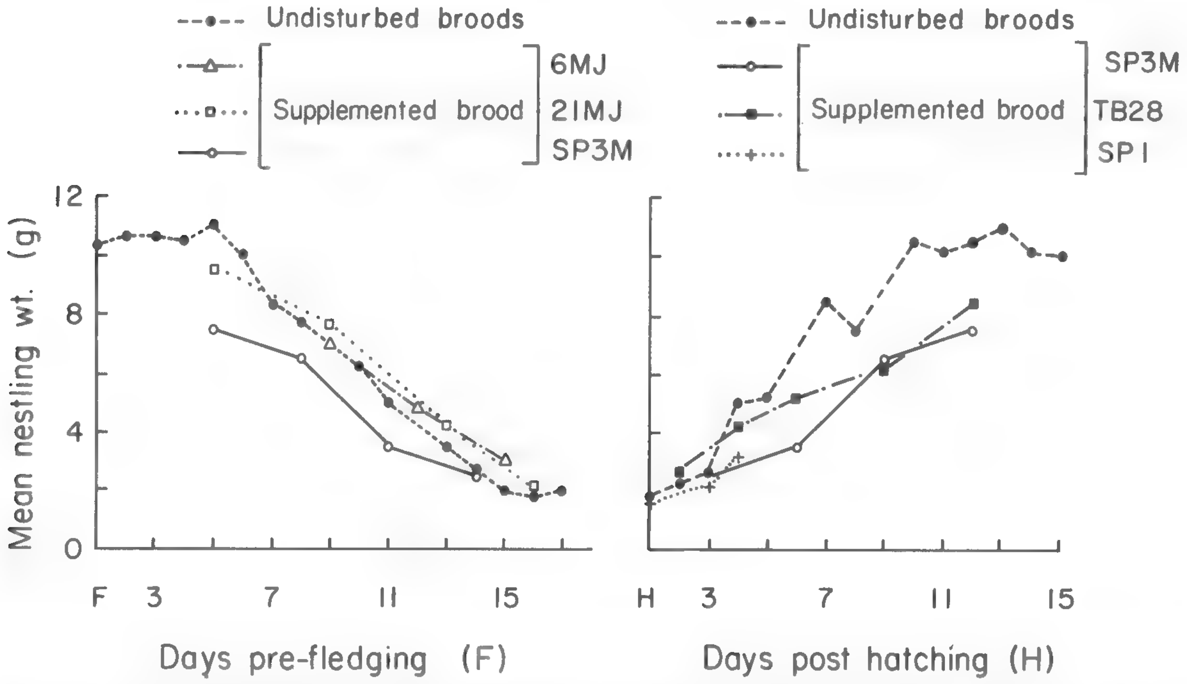


Figure 4. Unsmoothed growth curve for nestlings of *M. manacus* in undisturbed nests and in others supplemented with additional young in Trinidad, 1971. Two graphs are presented, because in many broods only one fixed point in time was known — either the hatching or fledging date. One brood (SP3M) had two known fixed points and appears in both graphs. F indicated the fledging day of all nestlings from single-egg clutches, synchronously fledged broods, and the first nestling to depart in asynchronously hatched broods. H is the day of hatching of all single-egg clutches and synchronously hatching two-egg clutches, and the first egg to hatch in an asynchronously hatching clutch.

statistically in five asynchronously hatched and three synchronously hatched broods (0.9 versus 0.3 gm, $t_6 = 2.160$, $p > 5\%$). Only two of the five asynchronously hatched broods had inter-nestling weight disparities which might potentially have been sufficient to promote unequal competition for food during a shortage (1 and 1.5 gm). The magnitude of the weight difference between members of asynchronously hatched broods was uncorrelated with the extent of asynchrony in the present small sample.

If, as seems likely, the female parent of an asynchronously hatched brood commences incubating before laying the second egg, some mechanism may operate to reduce the weight difference between the two offspring to a level comparable to that observed in synchronously hatched broods. In the three asynchronously hatched broods showing such parity in inter-nestling weight with synchronously hatched broods, the first hatchling gained as much before its nest-mate hatched as both chicks of a synchronous-hatching brood gained during the first one or two days of development. However, the second chick of an asynchronous brood in each case was 0.5 gram heavier on the day it hatched that either a synchronous brood-member or the first-hatching member of an asynchronous brood. Two of these second nestlings were 66.6 percent heavier than their brood-mates had been at hatching. In some asynchronous broods, the greater weight of the second nestling theoretically could have been due to its hatching from a larger egg, to accelerated development in the egg, or to preferential feeding by the female immediately after hatching (it was usually not weighed until a few hours after hatching). Only the last of these mechanisms is consistent with Lack's (1968) interpretation of the adaptive value of asynchronous hatching; but not all asynchronous broods were homogeneous for size, and I do not know whether my limited sample represents the population as a whole.

Synchronous fledging occurred in four of the eight broods accurately monitored for fledging; of the remaining four, three fledged at one-day intervals, and a two-day interval elapsed in the case of the final brood. This last fledging interval was probably atypical, however, since it occurred in a brood with an abnormally protracted nestling period.

Is asynchronous fledging adaptive or merely the consequence of asynchronous hatching? I ascertained the relationship between hatching and fledging intervals for only one brood, and both were one day. Synchronous fledging should promote family cohesion on leaving the nest and thus probably enhance the young's survival to a greater degree; for during the interval of fledging in an asynchronously fledging brood, the female may have to divide her time and attention between two separate localities, which seems likely to increase the probability of predation on the young. It thus seems likely that fledging on different days results, at least partially, from hatching at one-day intervals. The stage of development of flight feathers must determine readiness to fledge, since the inter-nestling weight difference in asynchronously fledged broods on the day before the first chick fledged was not different from that found in synchronously fledged broods ($t_5 = 1.463$, $p > 5\%$).

Asynchronous hatching could be adaptive in several ways. It spreads out the work-load of the nesting female by reducing the period during which she has to feed two nestlings simultaneously by as much as 21 percent in a nest with eggs hatching two days apart and young that fledge one day apart. In particular, it separates the immediate post-hatching stage of de-

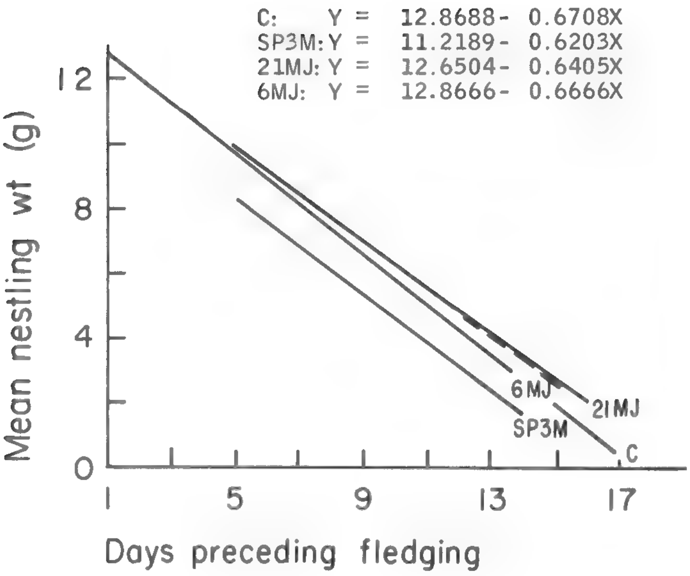


Figure 5. Regression of weight on age for nestlings in undisturbed and supplemented broods of *M. manacus* in Trinidad, 1971. Nests contained one nestling or two nestlings that fledged synchronously, indicated by C, and three supplemented broods in which one or two nestlings fledged. Day 1 is the fledging date of the first chick in supplemented broods. Regression lines fitted by least-squares method.

velopment of the two siblings, which Lack (1968) postulated is the most difficult time for the female to find an abundant supply of nutritionally suitable food for the young. The spreading out of the female's work load may have exerted an influence on male liberation. By commencing incubation of the first egg soon after it is laid, the female also reduces the duration of exposure of her older offspring to nest predators compared with the degree of exposure of offspring in synchronous broods.

Asynchronous hatching occurred in only a proportion of the broods studied. Hatching on different days may be an adaptation by which the female is able to gauge the availability of food in advance and adjust the onset of incubation and thus her parental work-load accordingly. Such adaptive behavior might be shown by any female as a direct response to food availability, or might be age-specific. A second possibility is that asynchronous hatching is a genotypic adaptation to seasonal variation in food availability, as has been postulated for the Great Tit (*Parus major,* Gibb, 1950). However, although Snow (1962a) demonstrated that later broods were more successful in my study area, no clear seasonal trend in the degree of hatching synchrony was apparent in the present sample. More extensive data are required before the significance of the intriguing phenomenon of asynchronous hatching and its relationship to the evolution of clutch size and unisexual brood-care can be fully evaluated.

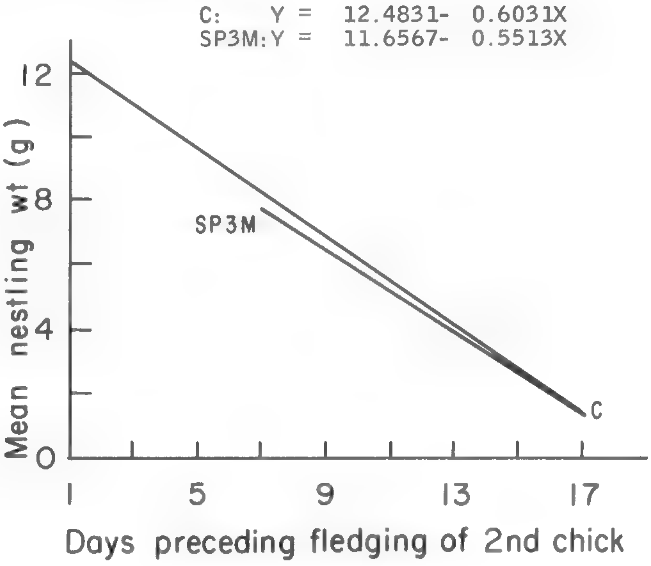


Figure 6. Regression of weight on age for undisturbed broods of two nestlings that fledged asynchronously (C) and one supplemented brood in which the two surviving nestlings fledged asynchronously (SP3M). Day 1 indicates the fledging date of the last nestling. Regression lines fitted by least-squares method.

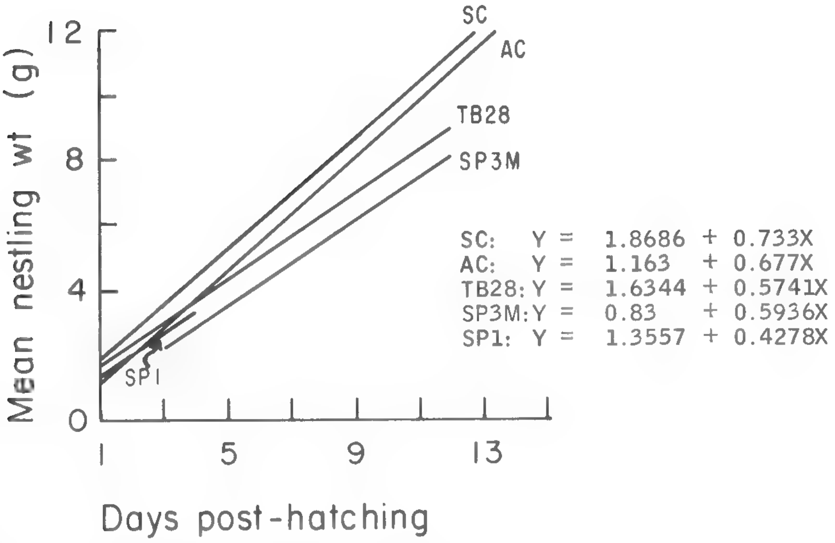


Figure 7. Regression of weight on age for undisturbed broods that hatched synchronously (SC) and asynchronously (AC) and three supplemented broods with known hatching dates (SP1, TB28, SP3M). Day 1 is the hatching date of all, or the first, eggs to hatch. Regression lines fitted by least-squares method.

Egg Size and the Incubation and Fledging Periods

Lack (1968) derived a proportionate egg-weight (the weight of the egg proportional to the weight of the bird) of 15.6 percent for *M. manacus* using linear dimensions given by Belcher and Smooker (1937). I derived a value of 13.1 percent from the weights of three fresh eggs from different clutches, but this value may closely approach, though not equal, Lack's figure, if allowance is made for the relative imprecision of my measurement (to nearest 0.5 gm). Lack contrasted the proportionate egg-weight of *M. manacus* with a value of 11.3 percent for other Passeriformes of the same body weight. He pointed out that the White-bearded Manakin has a relatively long incubation period of 19 days in relation to its 14-day nestling period. He suggested that the evolution of a large egg was adaptive in facilitating the production of advanced hatchlings, since suitable protein-rich food for tiny young may be sparse. The disadvantages inherent in this evolution would be the cost in energy of producing large eggs and the potentially dangerous extension of the laying interval.

The effective reduction of the nestling period achieved by extending the development within the egg is unlikely to be an anti-predation strategy because predation occurs equally in the incubation and nestling stages (Lack, 1966). It could have been adaptive in reducing the parental workload and in facilitating male liberation from the pair-bond, assuming that male liberation conferred a selective advantage on the female by enhancing her reproductive rate. Whatever the adaptive value of an extended period of development in the egg, the significant point for the present argument is that the large size of the egg may reduce the number of eggs a female can lay per clutch.

Nest Predation

That predators destroy as many nests with eggs as with young supports the idea that the nest predators found nests by searching "in likely places" rather than by observing parental visiting behavior, as explained earlier. The occurrence of some nocturnal nest predation (pers. observ.) supports this view. Snow (1962a) suggested that snakes are the principal nest predators of *M. manacus* in north Trinidad, but no concrete evidence is available. The cryptic near-silence of the nesting female and her young is in striking contrast with the noise generated at the nest of many temperate passerines and tropical birds using relatively safe nesting sites, such as the House Wren (*Troglodytes aedon*) and the Channel-billed Toucan (*Ramphastos vitellinus*, Lill, 1970). It suggests some strong non-ophidian predation pressures too, since snakes have rudimentary ears and hear airborne sounds poorly (Bellairs, 1969). Snakes have moderately good vision and elaborate olfactory receptors, which are probably both employed in searching for nests.

The nest is fairly inconspicuous because of its small size, coloration, and site. Selection favoring a small nest to reduce detection by predators searching visually would impose a limit on brood size. The brood supplementation experiments dramatically demonstrated that the nest of *M. manacus* is adapted for a maximum brood of two, since the experimentally augmented broods were extremely crowded and one nestling literally had to sit on top of the others.

Competition for Nest Material

Snow (1962a) reported strong inter- and intra-specific competition for nest material in *M. manacus*. The principal heterospecific competitor was the Ochre-bellied Flycatcher, *pipromorpha oleaginea*. Inter-specific competition is probably even stronger than he suspected, since some antbirds also used the nest lining material that grows only at the forest edge (Lill and ffrench, 1970). Furthermore, abandoned and unattended nests are soon pillaged for material, leading Lill (1974a) to suggest that the apparently unadaptive tendency of females to re-use depredated nests may relate partly to the difficulty of obtaining additional, suitable building material. Thus, competition for nest fabric also may favor, although in a minor way, a small nest size and thus limit brood size.

Food Availability for the Female

If parent birds can feed themselves in relatively few daylight hours with relatively small energy cost, they can spend correspondingly more time and greater energy feeding their young. This will facilitate either increased brood size or, where brood size is already maximal, the evolution of broodcare by one parent. Adult *M. manacus* are largely frugivorous and Snow (1962a) demonstrated that adult males can meet their food requirements in 10 percent of the daylight hours in north Trinidad, that the incubating female leaves the nest only briefly to feed, and that the fruits which constitute the major part of the adults' diet grow abundantly throughout the year. I agree with Snow that the plentiful food resources available to the female leaves the nest only briefly to feed, and that the fruits that conbreeding female are probably important in enabling her to rear the brood on her own, a conclusion also reached for polygynous weaverbirds (Ploceinae) by Brook (1962).

Various workers have discussed several other factors which may influence avian clutch size and, in some cases, male liberation. These include brood hyperthermia (Cavé, 1968), nest strength and structure (Snow, 1970 and 1972), and parental brooding capacity (Klomp, 1970). With the pos-

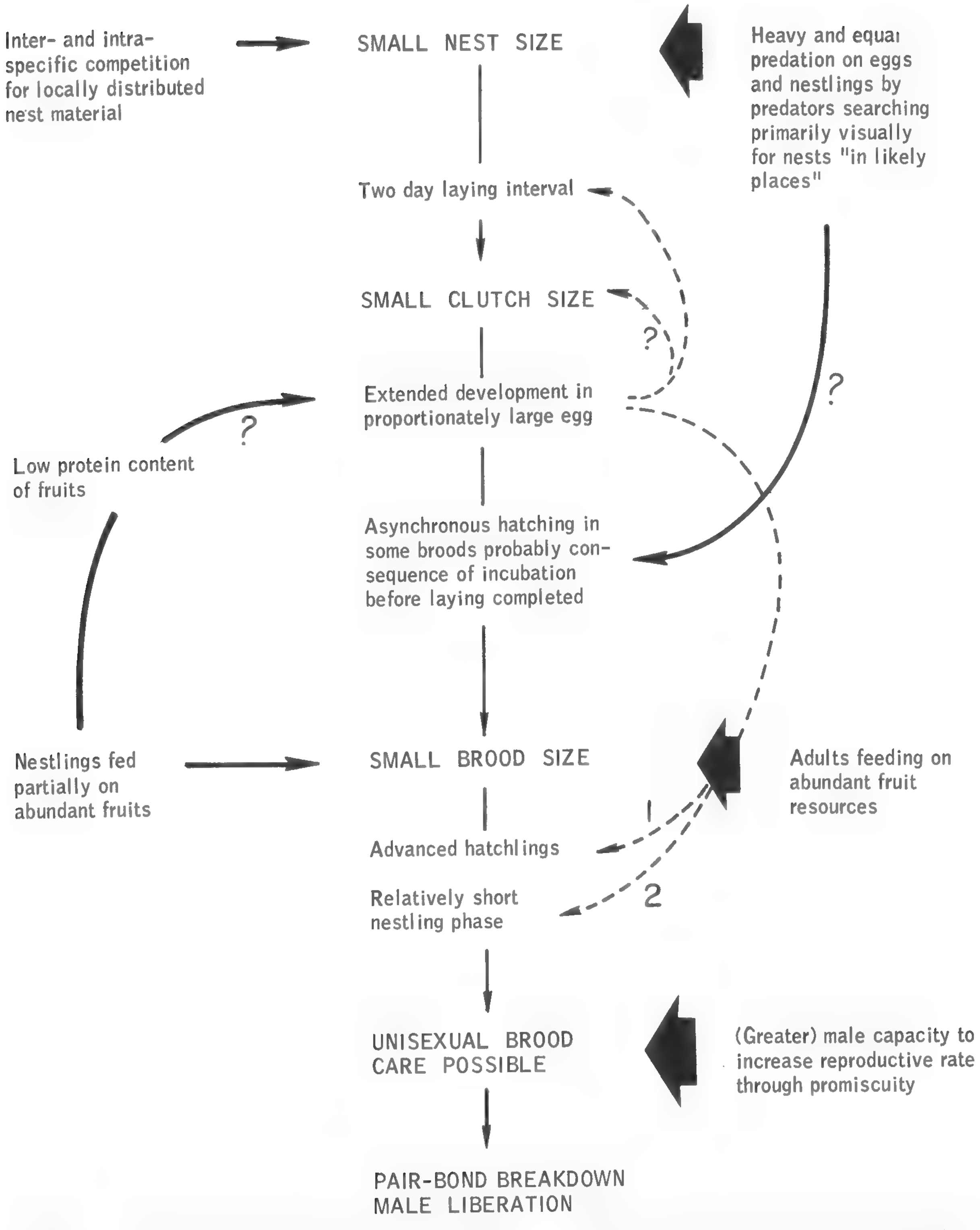

Inter- and intra-specific competition for locally distributed nest material
SMALL NEST SIZE
Heavy and equal predation on eggs and nestlings by predators searching primarily visually for nests "in likely places"
Two day laying interval
SMALL CLUTCH SIZE
?
?
Extended development in proportionately large egg
?
Low protein content of fruits
Asynchronous hatching in some broods probably consequence of incubation before laying completed
Nestlings fed partially on abundant fruits
SMALL BROOD SIZE
Adults feeding on abundant fruit resources
Advanced hatchlings
?
Relatively short nestling phase
?
UNISEXUAL BROOD CARE POSSIBLE
(Greater) male capacity to increase reproductive rate through promiscuity
PAIR-BOND BREAKDOWN MALE LIBERATION

Figure 8. A hypothetical model of the evolution of a low clutch size and male liberation in *M. manacus*. Stronger selection pressures are indicated by thicker arrows. The most tentative cause-effect relationships are marked with a query.

sible exception of nest strength, these seem unlikely to be of much importance in *M. manacus* with its open, shallow nest and tiny hatchlings partly covered with down.

Discussion

The significant percentage of insect food in the nestling diet, the apparent inability of females to adequately feed larger than normal broods, and, possibly, the existence of asynchronous hatching in some broods could be construed as supporting Lack's (1966) argument that availability of insect food for the nestlings is the critical factor limiting brood size in *M. manacus.* However, Skutch (1949) challenged Lack's theory of food availability and clutch size limitation for tropical, nidicolous birds. He commented on the similar clutch size of monogamous and polygamous species that differ in the degree of parental brood-care and that cohabit in neotropical evergreen forests. Haartman (1955) strengthened the challenge by providing similar intrageneric comparisons among European buntings and warblers with similar diets and feeding habits. If Lack's (1968) hypothesis is correct — that clutch size in birds evolved through natural selection to correspond with that brood size which produces, on the average, the most surviving young — it is unlikely that food availability for the nestlings serves as a common limiting factor for clutch size in entirely polygamous, nidicolous species. Were this so, natural selection would rarely have promoted absolute or partial liberation of one sex from a parental role.

Predation as a Selecting Factor

Nest predation seems to be the most plausible limiting factor of clutch size in the White-bearded Manakin. It accounted for 158 of the 183 clutches and broods that failed in Snow's (1962a) study, and for a comparable percentage of nest failures in my own investigation. Skutch (1960) records a similar nest failure rate of 87 percent for 23 nests of the Orange-collared Manakin in Costa Rica, probably due mostly to predation. High predation rates on eggs and nestlings will place a strong selective premium on any adaptation reducing nest predation, even if only by a small amount. A 10 percent decrease in the nest predation from 90 percent to 80 percent would double the reproductive rate (Snow and Lill, 1974). It seems probable that the principal nest predators find nests, at least in part, by looking in likely places rather than by watching the parent bird, and that some non-ophidian nest predators capable of utilizing auditory cues also are implicated in the high rate of nest failure.

The nest of *M. manacus* is well adapted to the normal brood size of two. It seems likely that selection favored a small nest less conspicuous to predators that hunt visually. Indeed, such selection may have occurred widely in the genera *Manacus* and *Pipra* in which small inconspicuous nests and high nest predation rates are common (Skutch, 1969; Lill, 1974c). A similar anti-predator strategy appears to an even greater degree in two related cotingids, the Rufous Piha (*Lipaugus unirufus*, Skutch, 1968 and 1969) and Bare-necked Fruit-crow (Béraut, 1970), in which the nest is so small that the incubating or brooding female entirely covers it and appears to be merely sitting on the supporting branch. If predators locate nests through developing a nest-site search image, the presence of a conspicuous male at the nest part of the time would probably increase nest detection only marginally. And if predators find *M. manacus* nests in this way, it seems unlikely that the greater conspicuousness of the male's plumage was a very important factor in the evolution of male liberation. The lack of striking epigamic plumage in liberated males of other manakin species, such as the Thrush-like Manakin (*Schiffornis turdinus*), supports this contention. Tropical birds reproduce less successfully on the average than temperate birds (Skutch, 1966), and predators of nests may have been a potent force in the evolution of low clutch sizes in the tropics, especially in forest birds with open nests.

The Evolution of Frugivorous Feeding

The evolution of largely frugivorous adult and semi-frugivorous nestling diets probably enabled the female to satisfy her own food requirements and feed, on her own, the maximum brood permitted by the small nest size. Several insectivores of roughly similar size and with similar nests and clutch sizes in the families Formicariidae and Sylviidae are monogamous, such as the Plain Antvireo (*Dysithamnus mentalis*), the White-flanked Antwren (*Myromotherula axillaris*), and the Long-billed Gnatwren (*Ramphocaenus melanurus*). Two similarly sized flycatchers a little smaller than *M. manacus,* the Ochre-bellied Flycatcher and the Slaty-capped Flycatcher (*Leptopogon superciliaris*), build pendant nests that probably are relatively immune from predation. The insectivorous *Leptopogon* is monogamous and has a clutch of two, whereas the frugivorous *Pipromorpha* has evolved unisexual brood-care and has a clutch of three or four (Snow, 1970). Another neotropical frugivore using a relatively safe nesting site, the troglodytic Oilbird (*Steatornis caripensis*) evolved a larger clutch than its close relatives but retained the pair-bond. However, the cool temperatures in the caves where this species nests apparently place a strong premium on almost continual incubation of the eggs and brooding of the small young. This could not be achieved by one sex alone, since the adults often have to travel long distances to feed at locally abundant but patchily dispersed fruit sources (Snow, 1962b).

The evolution of frugivory in the adult White-bearded Manakin probably facilitated male liberation more than partial frugivory in the nestling of this species. Skutch's (1969) account of the nesting of the Thrush-like Manakin indicates that the female may feed mostly insects to the nestlings, although adults take both fruit and insects. Similarly, in the promiscuous Capuchinbird (*Perissocephalus tricolor*), a cotingid, the largely frugivorous female feeds mostly insects to the young (Snow, 1972). Although I feel that the exploitation of the abundant fruit resources of neotropical forests played a significant role in the evolution of male "chauvinism" in many cotingids and manakins, the combination of a low clutch size and adult frugivory did not lead to liberation in all cases (e.g., the Purple-throated Fruit-crow, *Querula purpurata,* Snow, 1971). Once the female White-bearded Manakin could rear the maximal brood of two single-handed, the male's capacity to enhance his reproductive rate by copulating with other females would have promoted his total liberation from the pair-bond.

How do larger eggs, an extended incubation period, and asynchronous hatching fit into this theory of male liberation? It seems unlikely that the extended development in the egg — thus larger eggs and longer incubation period — represents an adaptation to reduce that period requiring the greatest energy of the parent (the nestling phase). In at least some clutches, an asynchrony of hatching extends the overall nestling period proportionately, although it reduces the period during which two nestlings are simultaneously present.

Fruit has a low protein content (Morton, 1973); and Lack (1968) suggested that extended embryonic development in *M. manacus* adaptively by-passes or reduces the early nestling phase when fruit is an unsuitable food for rapidly growing young. Since reduction of the nestling phase through extended development in the egg is often counterbalanced by an extension of parental care due to asynchronous hatching, and thus apparently confers no advantage in avoiding predation, the by-passing idea is plausible. However, Skutch (1969) also recorded extended laying intervals and incubation periods in some clutches of various antbirds that build similar cup nests and feed their nestlings animal food. Some of these species have proportionately large eggs. If Lack's (1968) hypothesis for an extended development in the egg in manakins is valid, we must conclude either that the protein content of the fruits fed to the nestlings is not the critical factor involved, or that the trait evolved in response to other selection pressures in the antbirds.

Asynchronous Hatching and Male Liberation

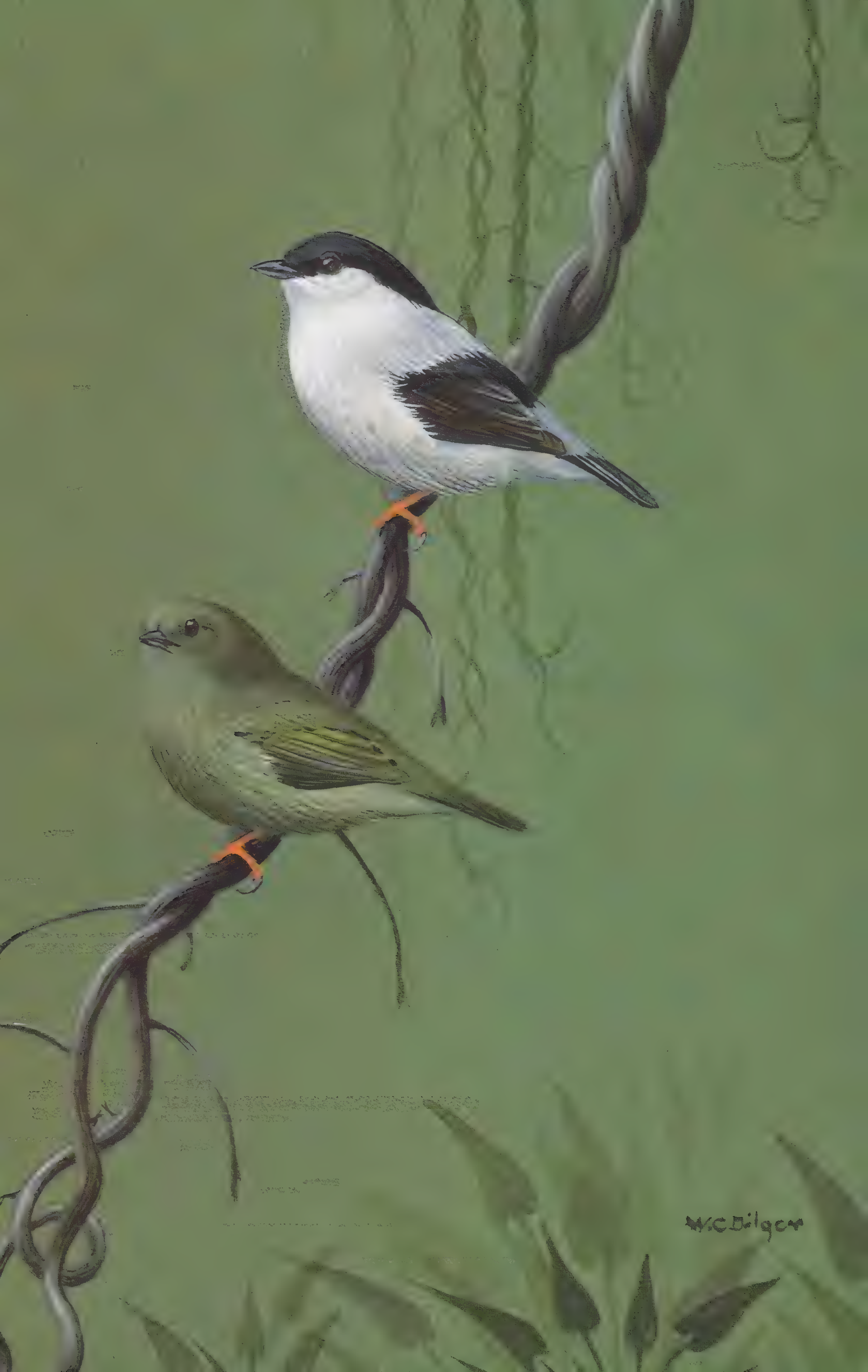
Asynchronous hatching might be considered either an adaptation that spreads out the parental workload during the nestling phase or merely the consequence of commencing incubation before completing the clutch. Such an early onset of incubation would reduce the exposure of the first egg, which is shielded from the view of arboreal nest predators during the laying interval. Its hatching period would be reduced in comparison with the first-laid egg in a synchronously hatched brood. According to this argument, one would have to suppose that food availability for nesting females with asynchronously hatched broods was sufficient to permit a significant reduction in the time required to collect food to form the second egg, but not by a whole day.

Judgment must be reserved on the significance of asynchronous hatching until more data are available to show how it is effected and how frequently it occurs in *M. manacus*. Similarly, the adaptive value of extended development within the egg will become clearer as further inter-specific comparisons become possible. I expect that such data will necessitate some revision of the speculations offered above. I have summarized the foregoing theory of the evolution of a low clutch size and unisexual brood-care in *M. manacus* in the speculative model shown in Figure 9.

Reproductive Rates

In general, avian clutch sizes and the number of breeding attempts per season are unlikely to be adjusted to mortality rates (Kipp, 1948; Rensch, 1938; Skutch, 1967; Wynne-Edwards, 1962) if they have been determined by natural selection (Klomp, 1970). It is also unlikely that adjusted reproductive rates have evolved frequently as biotic adaptations through selection between demes, or populations, because the conditions permitting such a mechanism to operate are rare in nature (Maynard-Smith, 1964; Williams, 1966). Adjusted rates could evolve in species exhibiting the group territoriality-nest helpers syndrome if such species turn out to be kin-selected. But plausible explanations of the phenomenon based on individual selection can readily be advanced (Lack, 1968; Williams, 1966).

Lack's (1966, 1968) concept of a reproductive rate adapted through natural selection to yield the maximum number of surviving offspring satisfactorily explains most of the known facts about avian clutch size. However, it is important to stress an implied, but sometimes overlooked or underemphasized, point in Lack's more recent discussions of this theory, namely that maximization is a long-term phenomenon that does not necessarily refer to the immediate production of young. This is particularly important


W.C Dilger

in considering why tropical birds have lower reproductive rates than temperate species, a subject of much argument in recent years.

Skutch (1949, 1967) observed that many birds living in stable tropical environments seem to be rearing fewer young than they are capable of raising. This is in accord with the maximal rate theory provided the long-term view is borne in mind. Williams (1966) points out that genic selection favors an optimum reproductive effort, which counterbalances immediate reproductive opportunities against the total opportunities inherent in the future prospects of the individual. The reproductive rate is adapted to the probability of mortality through natural selection operating over the breeding life of an animal. Snow and Lill (1974) stress that a high annual survival rate may favor a reduction in the amount of energy expended by a parent for each brood or during each season, if it enhances parental longevity. The reason for this is because the expectation of further life increases disproportionately with an increase in the annual survival rate. Recent evidence indicates that many neotropical forest birds, including manakins, have low annual mortality rates and far greater longevity than north temperate species (Snow, 1962a; Snow and Lill, 1974; Willis, 1972), presumably because of the relative stability of their food resources. Natural selection is thus more likely to maximize the reproductive rate of individuals of such species by what one can call the tortoise strategy ("slow and steady wins the race") and of individuals of temperate species by the hare strategy. Thus, the reproductive effort expended in a given season may be smaller than the maximum possible effort.

Cody (1966) suggests that tropical species with stable food supplies and consequently low annual mortality rates exist at saturation densities close to the carrying capacity of the habitat (*K*). This will accentuate the selection for characters promoting increased competitive ability and survival, often at the expense of the reproductive rate. Contrastingly, the seasonal fluctuation of food supplies in most temperate environments leads to high annual mortality and selection for an increase in the rate of population growth (called *r* selection). Cody's theory comes closer than most others to accounting for the low clutch size of most tropical birds, but one puzzling complication should be mentioned. If tropical species exist at saturation densities, as Cody claims, how do the tropics accommodate vast numbers of migrants each winter? Lack and Lack (1972) have recently shown that one of the two resident wood warblers in Jamaica expands its range of habitat in summer to include those occupied by migratory parulids between October and April. This type of ecological interaction between wintering migrants and residents is difficult to account for without postulating marked seasonal fluctuations in the food supply or the population density of the residents, which should promote increased *r* selection. However, too little detailed attention has been directed to the ecological relationships of migrants and residents in the tropics to indicate whether the range of habitats or niche-width of residents commonly undergoes restriction during winter due to the migrant influx. A further prediction that might be made from Cody's theory is that migrants, which must experience less seasonal fluctuation in their food supplies than temperate residents, would exist at population levels intermediate between those of temperate and tropical residents

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White-bearded Manakin (*Manacus manacus*). Painting by William C. Dilger.

and so would have an intermediate clutch size. The nature of their ecological relationships with tropical residents on the wintering grounds should exert an important influence on the magnitude of the difference between their population levels and those of temperate residents at the start of the temperate breeding season.

If the reproductive effort expended in a given breeding attempt is less than the maximum effort possible, it is clear, in retrospect, that the failure of parents to rear supplemented broods may not necessarily indicate that brood size is adapted to food availability for the nestlings, particularly in tropical forest species (Cody, 1971). Thus, in this investigation, the failure of female White-bearded Manakins to feed all members of supplemented broods adequately might have been due to a physical inability to collect sufficient food for the enlarged brood in the time available; but it could equally have resulted from the genotypic adaptation of their feeding rate to an optimal brood size of two, evolved in response to nest predation. Thus, the results of the present supplementation experiments do not necessarily contradict the logical deduction that food availability for the nestlings is unlikely to limit brood size when one sex has been liberated from a parental role.

When we re-interpret the results of some published experiments in which parent birds were unable to feed supplemented broods adequately, there is still some suggestion that food availability for the nestlings limits clutch size in many of the predominantly temperate species that are monogamous (Klomp, 1970). Significantly, some of the examples of birds successfully rearing supplemented broods (Nelson, 1964) are for temperate seabirds, whose food supplies are likely to be relatively stable and which are thus likely to be selected for on the basis of competitive ability (called *K* selection). One would expect that, on the average, monogamous species in which one sex (generally the male) plays a significant smaller part in feeding the nestlings, are less likely to have a clutch size adapted to food availability for the young. Such species often exhibit more pronounced sexual dimorphism. Presumably, this is partly because the "need" for cryptic plumage and behavior is reduced in the sex less involved in parental duties. One qualification of this hypothesis is that, in some of these species, the sex which feeds the young less may make a comparable contribution to their survival by defending a territory containing a significant percentage of the food resources required. But it seems clear that the reproductive rates of nidicolous polygamous species have evolved through genic selection and that food availability for the brood is unlikely to have determined their clutch size in most cases (see also Orians, 1969).

Summary

I examined the ultimate factors influencing clutch size and the evolution of unisexual brood-care in the lek-forming White-bearded Manakin (*Manacus manacus*), a species in which the promiscuous males play no part in rearing the young.

The nestlings eat fruit and insects, the latter averaging 50 percent of the diet. One or more nestlings in most artificially supplemented broods showed a retarded growth rate and a death from starvation occurred in one of these broods. Asynchronous hatching occurred in some broods. The

weight difference between the members of these broods at completion of hatching did not average greater than that observed in synchronously hatched broods; in three of five cases, the weight difference was insufficient to promote unequal competition for food between brood-members under conditions of food shortage. The proportionately large size of the egg may influence clutch size. I discussed the idea that the adaptive significance of the extended period of development in the egg may lie in "by-passing" an early nestling stage when it is difficult for the female to provide suitable food for her rapidly growing young.

The high rate of nest predation is effected by predators that do not find nests primarily by observing the nest-visiting behavior of the breeding female. Strong inter- and intra-specific competition for nest material exists. The abundance of the main constituent of the nesting female's diet, small fruits, enables her to meet her daily food requirements rapidly and at a low energy cost.

I argued that food availability for the nestlings is unlikely to be a common limiting factor of brood size in polygamous, nidicolous birds. A tentative model to explain the evolution of a small clutch, unisexual brood care, and male liberation in *M. manacus* proposes that heavy nest predation favored a small nest and thus limited the brood size to two. The evolution of frugivory facilitated unisexual brood-care, and the greater capacity of the male to increase his reproductive rate through promiscuity led to male liberation from a parental role.

I suggested that most tropical forest passerines have lower reproductive rates than temperate passerines partly because the stability of food resources and consequent low annual mortality favor a "tortoise" rather than a "hare" strategy of optimizing the reproductive rate. This strategy is further accentuated by the fact that such species may generally be *K*-selected rather than r-selected, although the influence of wintering migrants on population levels and food supplies of tropical species is poorly understood and may be a complicating factor.

Acknowledgments

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Least Bittern, *Ixobrychus exilis.* Drawing by Orville O. Rice.

THE ANTARCTIC TERNS OF ANVERS ISLAND

David F. Parmelee and Stephen J. Maxson

Photographs by the authors

The Antarctic Tern (*Sterna vittata*) is a little-known species inhabiting seashores in both antarctic and subantarctic zones of the southern oceans. It does not have the reputation of being a world traveler like its northern counterpart, the Arctic Tern (*Sterna paradisaea*). Some claim that Antarctic Terns are nearly sedentary, since they evidently remain close to the breeding sites even in the dead of winter where open waters persist. A few sightings far from land, however, suggest that Antarctic Terns may range more widely than earlier suspected. Present records show the species breeding south to just beyond 68° S Lat. on the Antarctic Peninsula. This study deals with one of the far southern colonies breeding on Anvers Island near the Antarctic Peninsula, at approximately 64° 45′ S Lat., 64° 05′ W Long. From 22 November to 12 December 1973, we concentrated on the behavior of adults during the phases of the breeding cycle concerned with the care of eggs and small young. We also made direct comparisons between the Anvers Island colony and others of the Antarctic Peninsula region and South Shetland Islands.

Itinerary

Under the auspices of the National Science Foundation United States Antarctic Research Program (USARP), we boarded the Research Vessel *Hero* at Ushuaia, Argentina, and on 15 November 1973 proceeded across Drake Passage enroute to the South Shetland Islands. Because of delays relating to mechanical problems with the *Hero*, our group had to abandon original plans for studying birds and seals in the pack-ice ecosystem off the Antarctic Peninsula. With our time at sea greatly reduced, we decided to spend our remaining days collecting specimens of birds and blood samples from seals while investigating new sites. We especially wanted to find a readily accessible nesting ground of the Antarctic Tern for future study.

At Stigant Point on King George Island during 18–19 November, we found a few flying terns but none nesting. At Harmony Cove on Nelson Island during 19–20 November, we observed 30 or more terns defending a nesting ground still covered with snow. Nesting on Nelson Island was reported earlier by Araya and Arvena (1965). We occasionally saw terns flying above the open water and ice floes of Gerlache Strait but failed to see nesting areas that we suspected were not far off.

Arriving at Palmer Station (Anvers Island) on 22 November, we were disappointed to learn that uncertain ice conditions in the bay precluded a detailed, day-by-day study of terns reportedly nesting on some of the outlying islands. But the discovery of a colony of more than 60 birds nesting on nearby Bonaparte Point prompted us to commence immediately a study of these birds. Although ice prevented our reaching the small islands near Palmer Station on more than a few occasions, we succeeded in assessing numbers and breeding schedules of terns nesting on Cormorant, Breaker, and Humble Islands during 25–26 November. Actually, Watson *et al.* (1971) had earlier reported terns nesting on Bonaparte Point as well as Cormorant and Breaker Islands. George A. Llano (pers. commun.) informed us of terns nesting on Humble Island.

On 12 December we departed from Anvers Island aboard the *Hero* and sailed back through Gerlache Strait, once again recording flying terns but not colonies. On 13 December we noted several pairs of terns apparently breeding at the abandoned British station within the flooded volcanic crater of Deception Island, where the species has been known to breed (Holgersen, 1957); and a colony of some 40 birds heretofore unreported (Watson *et al.*, 1971) at False Bay, Livingston Island. We also learned that the colony visited earlier at Harmony Cove had finally settled down to nesting. All observations on Antarctic Terns ceased when we entered Drake Passage on 13 December.

Study Area

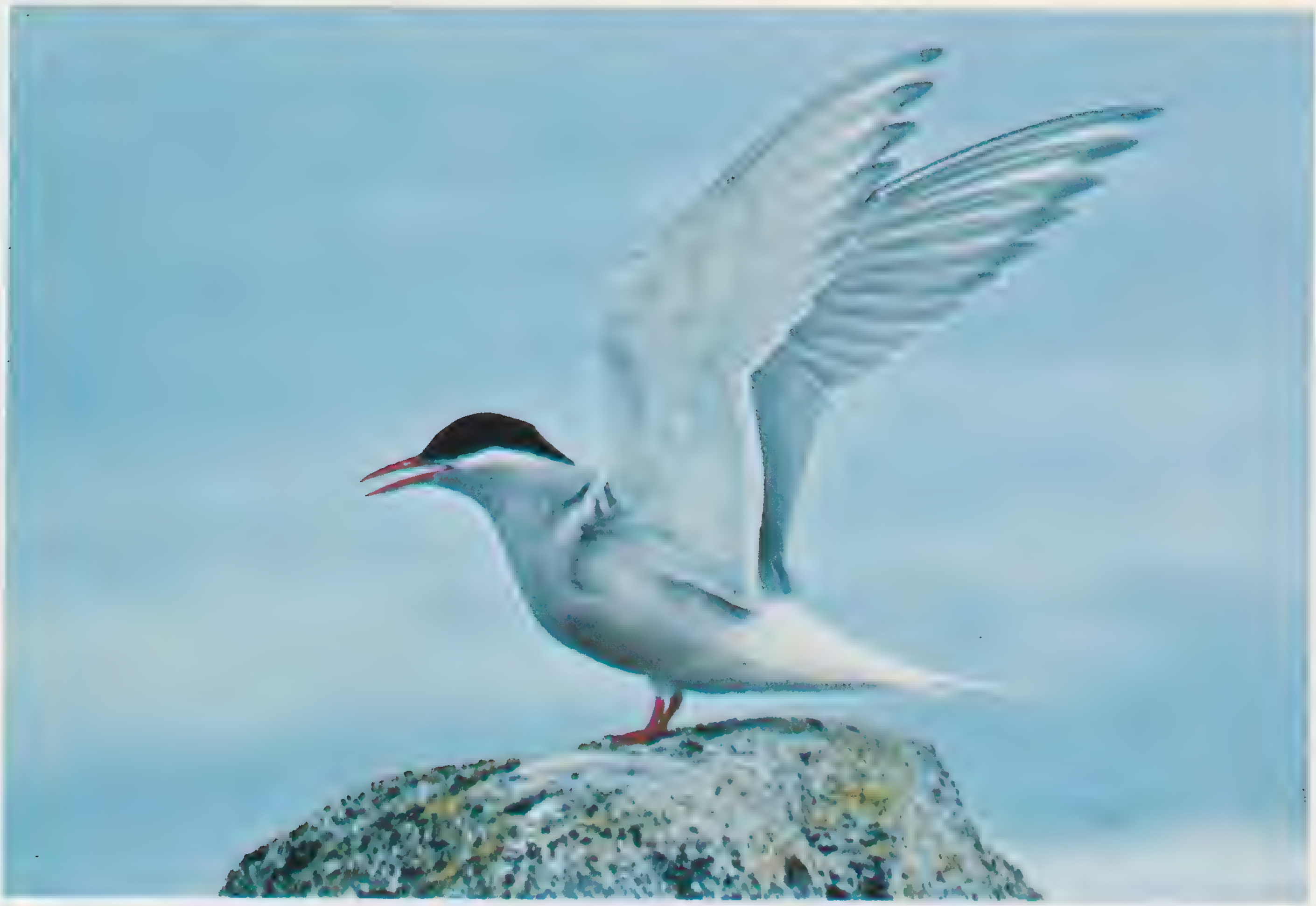
The study area was a finger-like projection of glacial accumulation that emerges from beneath the Anvers Island ice cap and extends some 1,200 meters into the sea as Bonaparte Point. A number of ridges 10 to 20 meters high and inundated with boulders crown this peninsula. During the austral winter, the valleys between the ridges and boulders fill with snow that slowly softens and disappears in spring, making walking difficult but not treacherous.

A narrow inlet extending all the way to the ice front isolates the peninsulas of Bonaparte Point and Palmer Station. The only suitable means of crossing this inlet is by a hand-operated chairlift suspended from a steel cable, since the overland route between the peninsulas is blocked by a crevassed glacier and the sea route often by ice floes. The shores of the inlet are fairly steep, and some cliffs rise from the sea on the Bonaparte Point side.

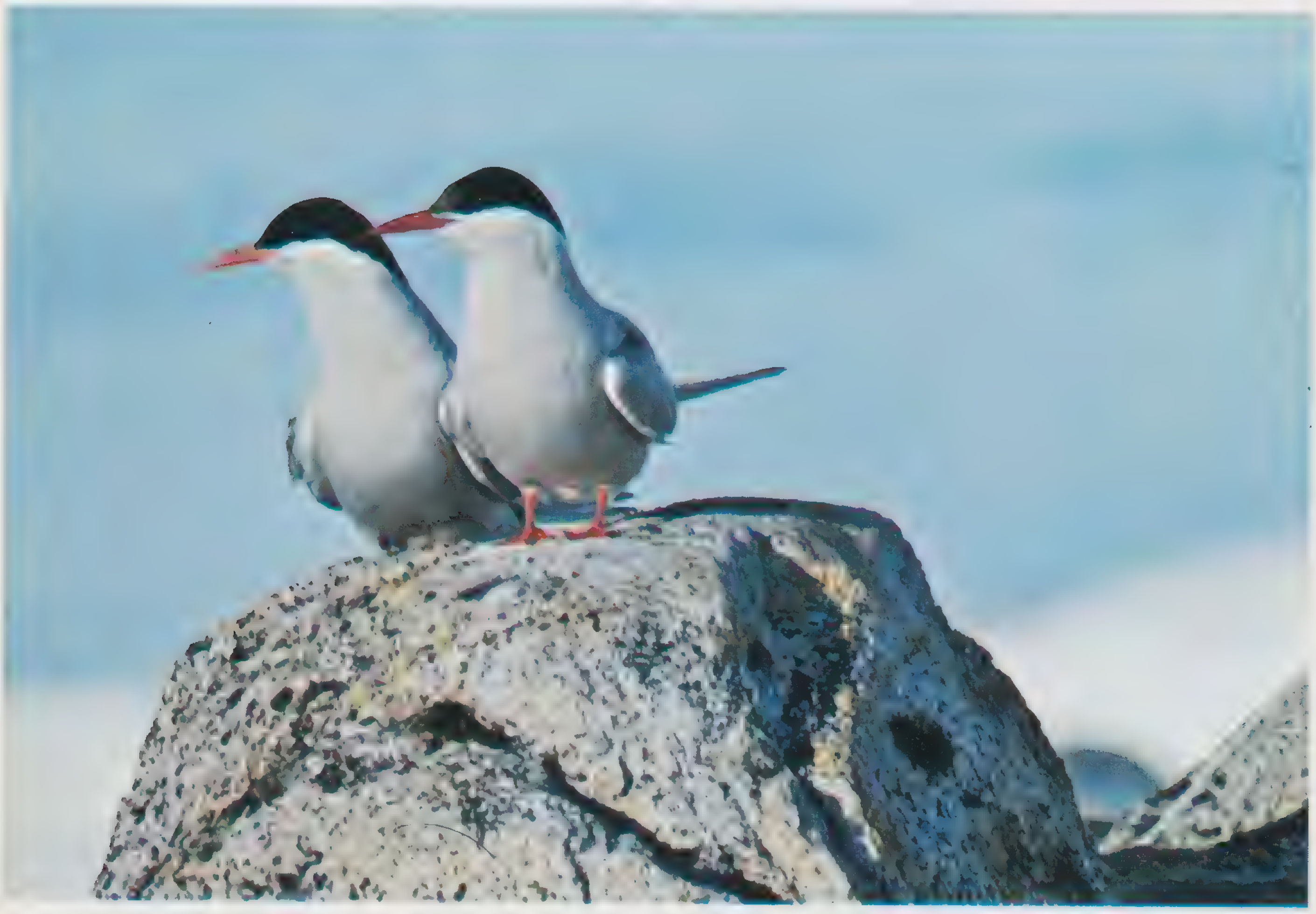
The dominant feature of the landscape is the glacier that rises precipitously at the head of the inlet for a height of 50 meters before continuing inland as an ice cap that nearly covers Anvers Island. The ice cap discharges its excesses through so many glaciers near Palmer Station that one soon is accustomed to the constant rumbling and cracking of ice both far and near.

With a single exception, the Antarctic Terns occupied several rocky areas below the glacier at the head of the Bonaparte Point peninsula. The main colony nested on the top and sides of a rock dome on the edge of the inlet across from Palmer. This nesting ground, encompassing some 300 square meters of exposed rock on 22 November, we called Area A. It contained 23 nests (Nos. 1–19, 30–33). A somewhat smaller and less definitive nesting ground farther inland and closer to the glacier we called Area B. Here the terns had 10 nests (Nos. 21–28, 34–35) on slightly exposed ridge-tops and boulders separated by fairly deep snow.

Several pairs nested apart from these concentrations. One pair (No. 20) nested on a narrow ridge-top fairly close to Area A; another (No. 29) on a flat rock at least 50 meters from Area B; a third (No. 36) on a sheer sea cliff very close to the glacier beyond Area B. A truly isolated pair (No. 30A) nested on massive rocks jutting out into the sea on the opposite side of the peninsula.



Antarctic Terns (*Sterna vittata*) on Anvers Island, Antarctica, December, 1973.
Photographs by David F. Parmelee.



Methods

We marked the nests by painting numbers on rocks near them. The eggs we marked with dots of red fingernail polish. Empty scrapes were marked in various ways but usually with colored wooden sticks that, if moved by the birds, indicated an interest in the site.

Nests, as a rule, were not difficult to find, although one had to look carefully to avoid stepping even on the marked eggs. With so much snow covering the ground early in the season, one could locate every occupied scrape by systematically walking back-and-forth across the rocks. Adults in defense of eggs invariably betrayed a nesting ground. We believe that we found every tern egg on Bonaparte Point.

We easily trapped adult terns by pulling a string that dropped a net stretched over a wire hoop on the incubating bird. We caught and marked one adult at each of five nests (Nos. 20, 21, 27, 29, and 35). The plumage of each bird was painted in various ways for easy field identification. We marked the bills and toes of newly hatched chicks with fingernail polish.

A canvas blind was built at Palmer Station for our use. After several trial runs, we placed it within Area B, to allow close views of several nests with marked birds.

Nesting Habitat

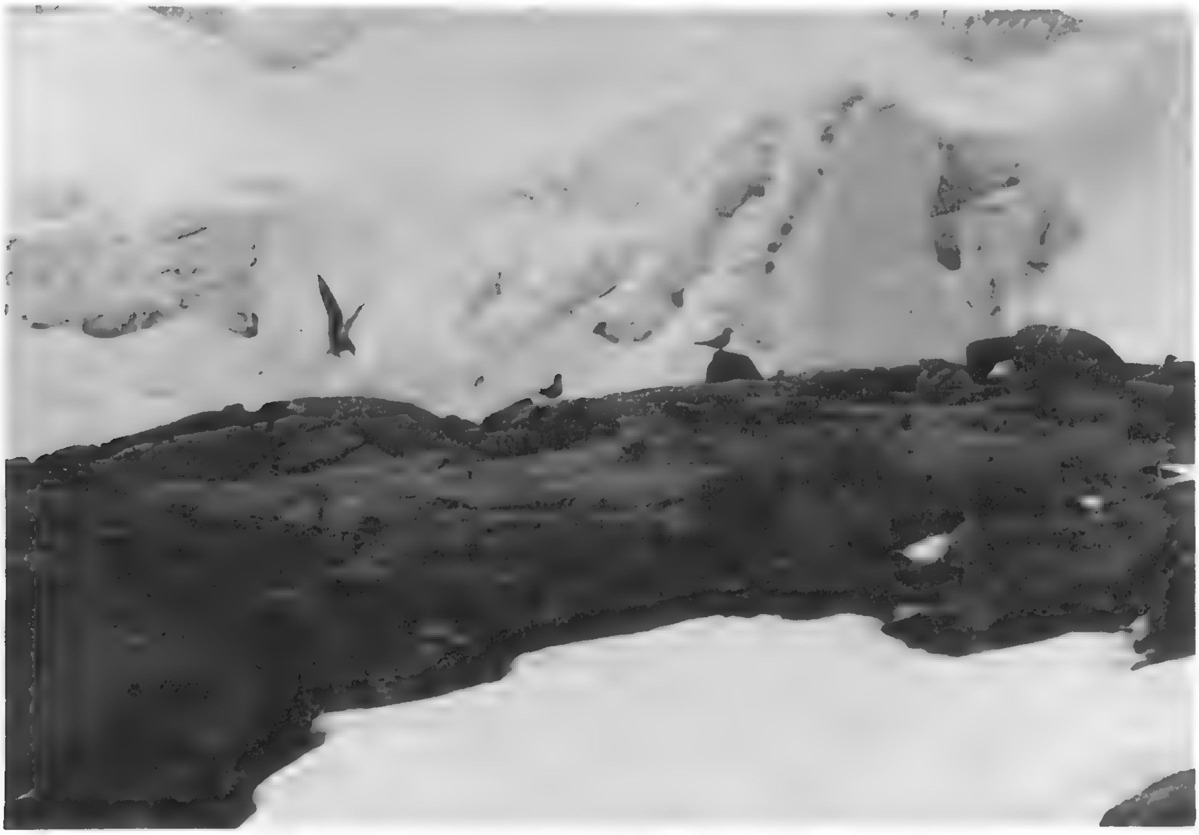
The Antarctic Terns of Anvers Island, and small islands close by, lay their eggs either on ledges of fairly precipitous cliffs overlooking the sea (Figure 1) or short distances inland on the tops of exposed rocky ridges (Figure 2). Many rocky sites inland are barely emerging from deep snow by the time egg-laying is underway. The exposed surface slowly increases with the thaw until, by hatching time, as much as 30 percent or more of the land may be snow free. Fresh snow occurs most any time, occasionally blanketing exposed surfaces completely; but it soon disappears without apparent damage to tern eggs.

The nest is a slight depression in bare rock or in a thin layer of soil and vegetation on rock (Figure 3). Most nests contain small stones, bits of soil and vegetation, or empty bivalve shells, all in disarray and presenting the appearance of a scrape. Although we did not witness the making of a scrape, we many times saw nesting birds scratching and picking at the pebbles before settling down to incubate. From this observation, we concluded that scratching or scraping activity probably takes place at the nest prior to egg-laying, although this point needs confirmation.

All nesting areas visited had a surplus of scrapes, indicating that some scrapes are not used every year, although conceivably some may be used repeatedly. Observations extending over several years at a given colony are necessary.

Since they favor rocky prominences and mostly avoid low-level beaches of sand, smooth stones, and shells, nesting Antarctic Terns differ from Arctic Terns and others in the family. Antarctic Terns do occupy the beach habitat in some areas, despite the presence of high rocks nearby. The colony breeding at Harmony Cove on Nelson Island inhabitated a low-level area with only a few scattered, flat, rocky prominences just beyond the beach. One nest was situated in gravel and one in beach litter, but the remainder of the seven nests seen were on the little prominences, clearly indicating a preference for rock in an otherwise typical beach habitat. According to Courtenay-Latimer (1957), the Antarctic Terns breeding off Cape Province, South Africa, breed in beach habitat alongside Roseate Terns (*Sterna dougallii*). Antarctic Terns of Tristan da Cunha, following the introduction of rats, evidently abandoned the habit of nesting on sandy beaches for the most inaccessible ledges, often on isolated stacks (Elliott, 1957).

Figures 1 and 2. The rocky cliffs along the shore of Anvers Island (*above*) provide nesting sites for the Antarctic Tern. The terns also rest short distances inland on the tops of exposed rocky ridges (*below*).



Pre-laying Period

Most tern eggs at Bonaparte Point had been laid by the time we first visited the study area. Still hoping to observe early phases of breeding, we counted heavily on certain pairs repeating the breeding cycle following predation of their clutches; but we found no evidence that these terns ever replace lost eggs. We did not see, or at least recognize, any pre-laying behavior of terns on Bonaparte Point that year.

Antarctic Terns arrive at the nesting ground at times when deep snow covers everything including the highest prominences. Instead of looking for new nesting grounds, they remain attached to the old one even for long periods until the familiar sites open up. That the birds show unusually strong affinities for traditional nesting grounds can be judged by the following experience:

At Harmony Cove on Nelson Island, during 19–20 November, we observed as many as 30 terns defending a snow-covered stretch of raised beach that later proved to be a nesting ground. Despite the snowy landscape, the birds circled excitedly over the area and occasionally directed shallow dives our way. They remained throughout our stay, although individuals came and left by way of the open sea. From this flock we collected four adults.

Not far from the tern nesting ground incubating penguins, petrels, and gulls already occupied exposed boulders, rocky outcrops, and rugged sea cliffs; but even the uninhabited areas of these seemingly favorable sites held no attraction for the terns. We revisited Harmony Cove on 13 December that year and found the tern area nearly free of snow. All nests seen then had fresh or nearly fresh eggs, at a time when hatching was peaking at the more southerly colonies.

Whether many of these terns skip breeding altogether when traditional nesting grounds fail to open up is speculative. Arctic Terns experience nonproductive years in the Canadian High Arctic where the annual snow cover and subsequent thaw varies locally as well as generally from year to year. Of 100 or more Arctic Terns seen by Parmelee (unpublished notes) at a nesting ground on Brooman Point on Bathurst Island, only three pairs defended nest sites on 22 July 1968. One nest held a single fresh egg despite the late date.

First-year Birds at Breeding Sites

Of great interest to us was the presence of first-year terns at the Bonaparte Point breeding colony, since we had never encountered first-year birds at any of many Arctic Tern colonies visited in the Canadian Arctic. The young Antarctic Terns were readily distinguishable from the brighter adults by their dull reddish-black bills and conspicuous white foreheads and underparts. They usually roosted during the evening and early morning not far from Area B on the uppermost surfaces of a ridge nearly buried by snow below the glacier. Since adults occasionally roosted with them, and because of their skittish nature, we failed to make accurate estimates of their numbers each day. Our records show that as many as 30 first-year terns roosted there from 22 to 27 November, after which their numbers fell off sharply. On 2 December we noted a roosting flock of only three birds. That same day a flock of about 20 young terns came in from the sea, passed low over the roosting rocks, and continued up and over the glacier, finally disappearing altogether. We saw none thereafter.

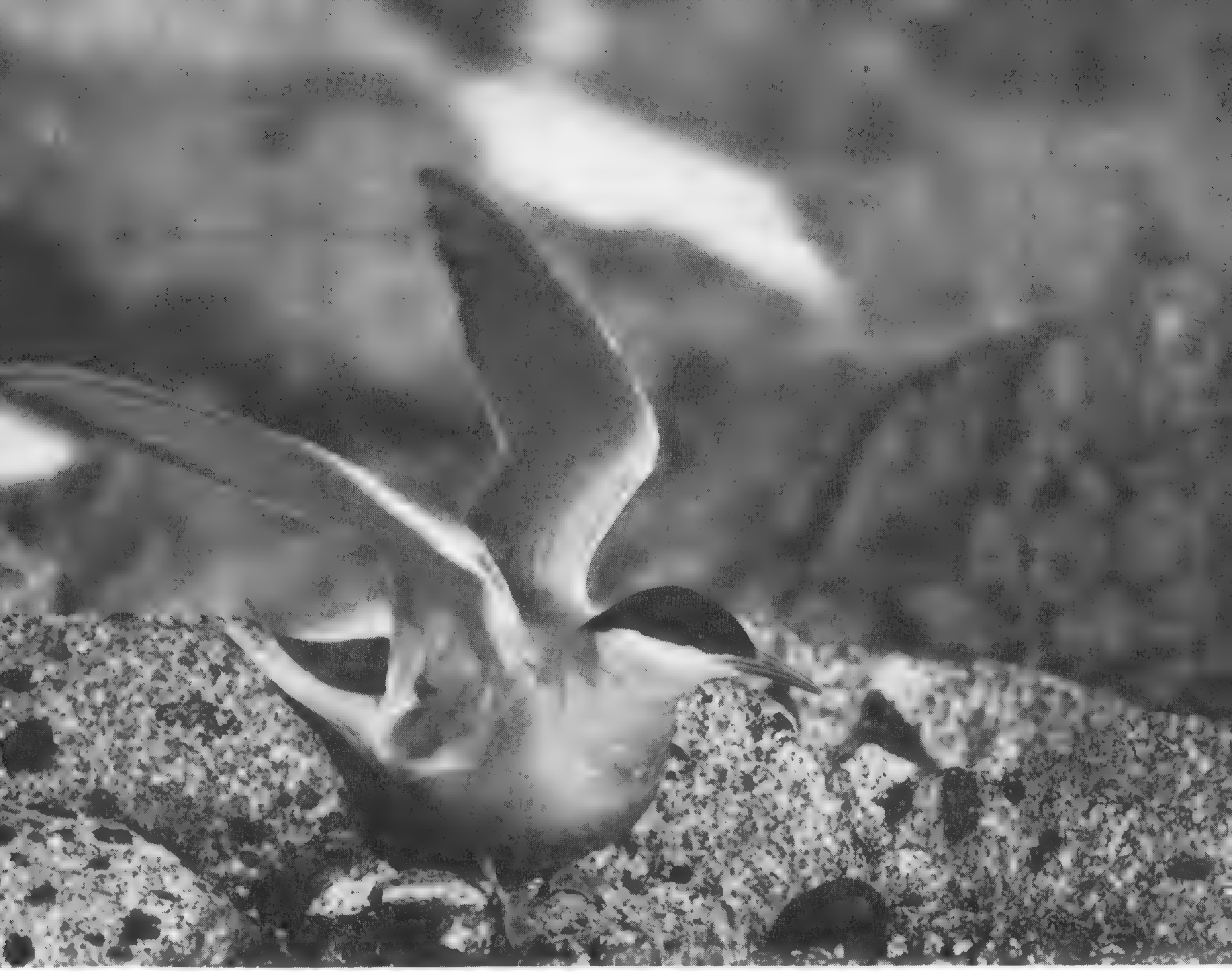


Figure 3. An Antarctic Tern stands before its nest, a slight depression in bare rock.

Earlier, the young terns often had flown with adults above the nesting areas, but we rarely saw them land near nests. When they did, the nesting adults swiftly drove them off. Whether the first-year terns are responsible for a number of single eggs dropped and quickly abandoned in the nesting areas is not known. No eggs showed up at the roost, though the presence of old scrapes indicated that the place had been used formerly as a nesting ground. A young male collected at the roost had small testes.

The Bonaparte Point colony with its attachment of young terns was not exceptional. When visiting Cormorant Island on 25 November, we found at least 50 young birds occupying a sea cliff adjacent to a nesting area. Although we failed to see a single young tern at the breeding sites on Breaker and Humble Islands on 26 November, our visit was far too brief to be conclusive. We did note one young tern among the many adults seen at False Bay on Livingston Island on 13 December.

Egg-laying and Incubation Time Intervals

Of the 30 nests marked in the study area on 22 November, the first day of observation, only three (Nos. 9, 16, and 19) had incomplete clutches. Twenty pairs had completed two-egg clutches, and two pairs, one-egg clutches. Single eggs at four nests (Nos. 6, 8, 15, and 28) evidently were abandoned and we considered them aborted attempts at nesting (discussed below). A two-egg clutch (No. 32), found within the colony on 23 November, likely had been completed by the 22nd. Another (No. 36) found far outside the main colony as late as 2 December may or may not have been completed by 22 November.

Since we had no data on the laying of the first eggs at Nests 9, 16, and 19, we could not determine the time interval between laying of eggs. It was at least 24 hours at Nest 9, 33 hours at Nest 16, and 29.5 hours at Nest 19. By marking empty scrapes we were able to determine a fairly precise interval between laying of the first and second eggs at Nest. 30. The first egg was laid in the scrape during 06:30 to 10:00 hours on 23 November, and the second egg during 10:30 to 11:30 hours on 25 November — an interval of 48.5 to 53.0 hours, or about two days. The only additional eggs laid in the study area after 22 November were singles that were immediately abandoned (Nests 31, 33, and 34).

In marking the second (last) egg at several nests (Nos. 9, 16, 19, and 30), we attempted to determine the incubation period, that is, the interval between the laying and hatching of the last egg of the clutch. Predators destroyed Nests 9 and 19 before hatching. Since the eggs of Nests 16 and 30 had not hatched by the time of our departure, we placed the last egg of Nest 16 and both eggs of Nest 30 in an incubator before leaving Anvers Island on 12 December and recorded their hatchings at Palmer Station.

The last egg of Nest 16, laid between 03:00 and 06:00 hours on 24 November, hatched at 13:30 hours on 17 December, a period of 23 days and 7.5 to 10.5 hours. The first egg of Nest 30, laid sometime between 06:30 and 10:30 hours on 23 November, hatched at 08:30 hours on 17 December, a period of 23 days and 22 hours to 24 days and 2 hours, or approximately 24 days. The second egg of Nest 30, laid between 10:30 and 11:30 hours on 25 November, hatched at 09:00 hours on 18 December, indicating a period of 22 days and 21.5 to 22.5 hours, or approximately 23 days. From these data, it appears that the period of incubation for the species is close to 23 days and that incubation at one nest (No. 30) commenced one day after the laying of the first egg.

Since the terns are off the eggs much of the time in a cold environment, incubation time probably could be reduced by warming the eggs artificially for the entire period. In the natural state, the period probably will average between 23 and 24 days.

Until now, egg-laying and incubation periods remained unknown for Antarcatic Terns. The incubation period seems fairly consistent with other *Sterna:* Forster's Tern (*S. forsteri*), 23 days (Bent, 1921); Common Tern (*S. hirunda*), 21 to 30 days, average of 25.7 days (Austin, 1967); Arctic Tern, 20 to 21 days (Parmelee, 1967); Roseate Tern, 21 to 26 days (various authors in Witherby, 1941); Sooty Tern (*S. fuscata*), 26 days (Watson, *in* Witherby, 1941); Least Tern (*S. albifrons*), 19 to 22 days (Witherby, 1941); Sandwich Tern (*Thalasseus sandvicensis*), 21 to 24 days, usually 23 (Chestney, *in* Witherby, 1941).

Given the egg-laying and incubation periods, and an early hatching date, we are able to determine that in 1973 egg-laying on Bonaparte Point probably began about 11 November, 11 days before our study began. Egg-laying probably peaked during 14 to 18 November, judging by the number of eggs that hatched between 10 and 14 December. Egg-laying at nests attended by adults continued until 25 November, indicating a spread of two

Antarctic Tern, *Sterna paradisaea*, in flight. Painting by David F. Parmelee.

weeks. Counting an abandoned egg that was laid as late as 27 November, the spread was at least 16 days and is apparently much greater at the more northern latitude of Snares Island (Stead, 1948).

Clutch Size

Antarctic Terns reportedly lay one to three eggs per clutch. One-egg clutches seem to be the rule on certain northern islands (Oliver, 1955). We did not see a single three-egg clutch on Bonaparte Point or elsewhere. Of the 37 nests observed in the study area, 27 had two eggs and 10 had one egg each. Of the 10 with single eggs, seven were abandoned from the start. One accidentally destroyed by us on 22 November contained no embryo and apparently had been abandoned. Considering only eggs that were incubated, the ratio of two-egg clutches to one-egg clutches was 27:2.

Why so many single eggs are deposited in nest scrapes and then quickly abandoned is a puzzling question. Conceivably, these abandoned eggs are aborted attempts at nesting by immature birds that stay close to the breeding ground, but we do not have any evidence to support this. In the beginning, we thought that single eggs were abandoned by adults attempting to nest too close to others. But this simply was not true of three nests that were fairly isolated from active nests. Our record indicates that these single, abandoned eggs are laid over a span of days. The last recorded by us was laid on 27 November (Nest 34). Whatever the reason for the abandoned single-egg clutches, one has to take them into account in discussing clutch-size. In our opinion they introduce a serious bias. For this reason, we make no attempt to assess clutch-size in the tern colonies visited on Cormorant Island and elsewhere.

Role of the Sexes in Care of Eggs and Young

Nest Attendance

In marking one bird of a pair at each of several tern nests, we soon determined that both sexes attended eggs. Not so obvious was the extent to which each parent incubated. From the beginning, we felt that one sex was on the eggs more than the other, but this was not easily determined because the sexes looked so much alike. Our best information came from Nest 35 where we observed the birds daily from 3 December through 10 December, and on 11 December collected one of the pair for positive sex identification.

Throughout the seven-day period, we made two- to three-hour observations during each of four designated times (24:00–06:00 hours; 06:00–12:00; 12:00–18:00; 18:00–24:00). This method gave us fairly good coverage of the 24-hour period. Of a total of 56.5 hours of observation, the female sat on the eggs 42.7 hours or 75.6 percent of the time. Observations at other nests with marked birds clearly indicated that one of the pair incubated much more than the other, but we were not certain of the sex.

Nest Defense

The marked bird at Nest 35 was the male. When not incubating, feeding, or chasing terns and skuas, it stood guard, at times within a few feet of the nest, but more often at a favorite perch 30 meters away. Since Nest 35 was more isolated than others of Area B, the male ranged more freely than its neighbors that nested close together. Where the terns nested really close together, the nesting spot defended by the pair was often only a few square meters in size. The bird defending such a small area was compelled to perch close to its incubating mate. Whether the defended ground was large or small, both members of the pair defended it viciously.

The tern on guard often challenged its neighbor with threat postures, calling loudly, pressing its body forward with tail up and nearly vertical at times, and with bill turned down; wings, although closed, were held low, somewhat away from the body. The neighboring tern assumed a similar Bill-down Threat display (Figure 4). As a rule, the birds threatened for only a few seconds, although the threats were often repeated. Sometimes the threat lasted a minute or more. Occasionally, threatening birds attacked each other with bold fury, though no apparent injuries ensued.

Terns flying low over the colony invariably elicited response. The bird on guard threatened as described above, except that now it pointed its bill skyward as well as downward. With tail and bill up, the body took on a peculiar bow-shaped appearance. Sometimes the attending bird leaped into the air to give chase. The incubating bird also assumed a Bill-up Threat display, even while on the eggs. Not infrequently, it left the nest to chase. The chases often resulted in aerial fighting. The space above the colony was so hotly contested that birds leaving or returning to nests often become entangled in mid-air.

So much of the tern's energy was spent calling, threatening, or chasing, that quiet spells seemed exceptional. On rare occasions, all attending birds perched peacefully near their incubating mates.

Nest Relief

Nest relief, or changeovers at the nest, by members of a pair were highly variable and took place at irregular times. The simplest changeover occurred when the incubating bird suddenly flew from the eggs and was replaced by the mate some time later. Although changeovers of this sort were common, they probably would have passed unnoticed if we had not marked the birds.

Another simple changeover took place without ceremony when the attending bird settled down on the eggs immediately after its mate walked off. Sometimes the attending bird with the urge to incubate attempted to nudge its mate off the eggs. It did not always succeed, for the incubating bird determined when changeover took place.

For reasons not at all clear, the incubating bird (usually the female at Nest 35) frequently picked pebbles, bits of lichen, and soil, and methodically tossed each item to one side or the other and, not infrequently, back over its shoulder. The picking and tossing continued for several minutes until eventually the bird stood up and walked off the eggs. Usually the bird continued to pick and toss in the vicinity of the nest until the attending mate went directly to the eggs. And the displaced bird usually did not fly off until after its mate had settled down.

At times the incubating bird picked and tossed without showing signs of leaving the nest, but the picking and tossing often preceded changeover. On rare occasions, the attending bird presented a small fish or minnow to the incubating mate, resulting in changeover several times. However, we doubt that minnows have much of a role in changeover.

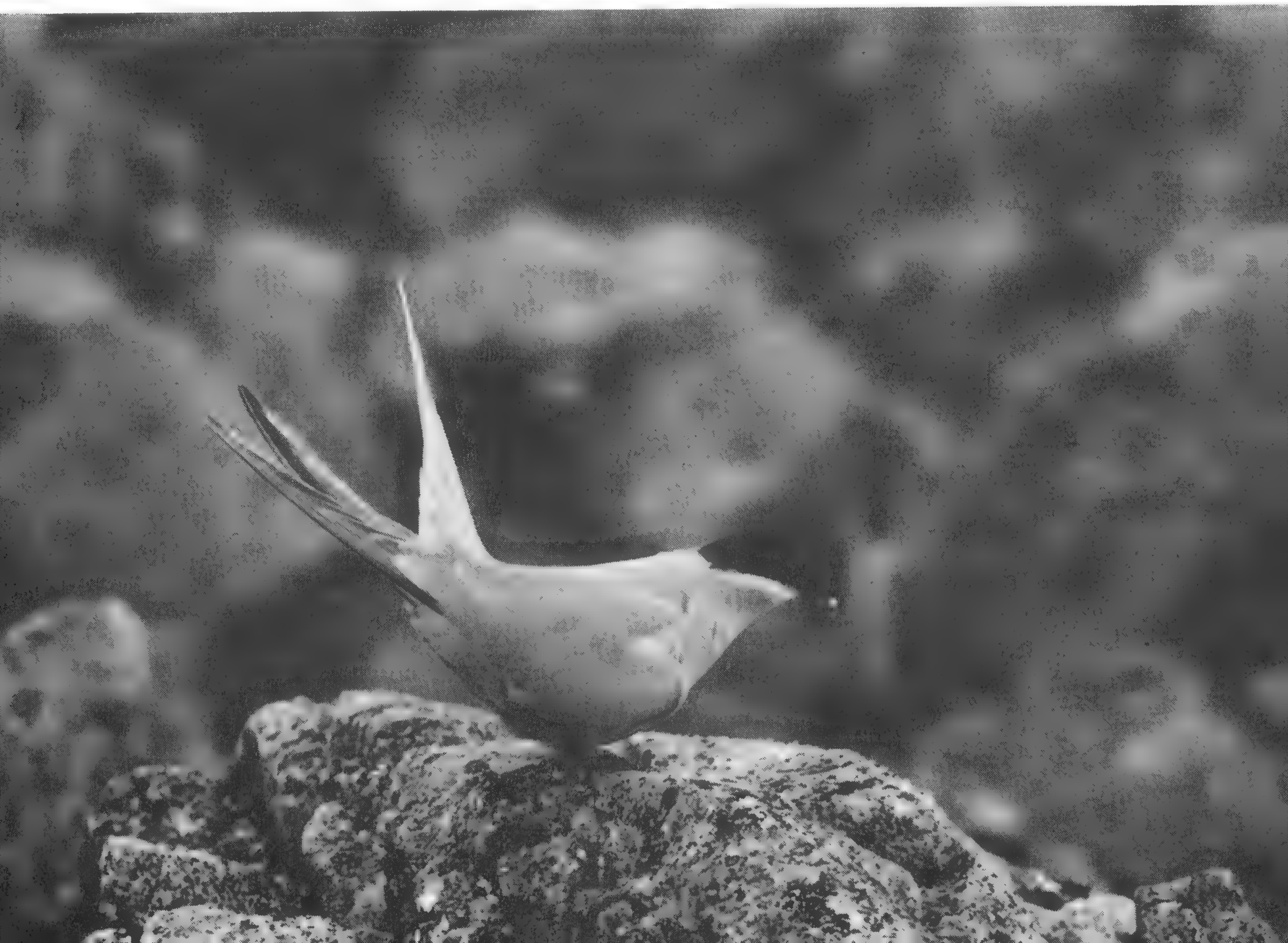
Before settling down to incubate, the terns often kicked pebbles out of the scrape with vigorous, deliberate backward thrusts of their legs and feet. Pebbles and other tiny objects within and outside the scrape are worked over many times during the course of incubation. So few pebbles occur on the austere breeding ground, that one would hardly suspect their importance.

We noted no great change in the behavior of the adults following hatching of the chicks, though our observations spanned only a few days. Both sexes brooded, the female seemingly the most. The male remained away from the nest for longer and longer periods, probably because of feeding commitments, but the point needs to be verified. When the parent arrived at the nest with food for the chicks, a brief greeting ceremony took place. Both adults pointed their bills and tails upward momentarily. Threat postures and changeovers appeared no different from those seen earlier.

Hatching and Care of Chicks

The first tern chick on Bonaparte Point hatched at Nest 24 (Area B) at 04:05 hours on 6 December. Its brooding parent immediately assumed a different appearance. No longer the quiet, sleek-plumaged individual that tended eggs, it now squirmed and frequently changed position with feathers

Figure 4. Antarctic Terns often guard their territories with a Bill-down Threat Display, in which they call loudly while holding the tail up, drooping the wings down and away from the body, and pointing the bill downward.



generally disarranged and puffed out in places. The second chick, about two days younger than its sibling, hatched during 08:00–09:00 hours on 8 December. Since our blind had been placed close to Nest 24, we had an unusually good view of these two young. We were especially interested in their movements, feedings, and growth rates.

Within five hours of hatching, the small chick frisked about in the nest, raised its head and opened and closed its bill in begging food. It also called at this time, although we did not record the kinds or frequency of calls. The calling subsided with feeding and picked up again an hour or so later.

The first chick moved and called a lot the first day, but we did not actually see it leave the nest scrape until the second day, when 35.5 hours old. Thereafter, it left many times, although at first it ventured forth only a few centimeters before quickly returning to be brooded. The small downy chick chilled rapidly except during unusually mild spells when the parent, without any pretense of brooding, watched over it from a rock perch. Whether the chick under cold stress solicits assistance from its parents was not determined, but adults brooded faithfully when temperatures dropped, sometimes immediately following a rise in wind or the sudden disappearance of the sun behind clouds.

The first chick was still being brooded at the scrape when its sibling hatched. When 60 hours old, it ran out as far as 30 centimeters. By 72 hours, a definite change in its behavior had taken place. Not only did it run from the scrape when the brooding parent left suddenly, it now hid among rocks nearby. In time, both chicks left the nest together and returned to be brooded, but the older and much stronger sibling wandered farther and farther afield. Nevertheless, it was compelled to return to the nest because the adults did not brood outside the scrape until later. Otherwise, it likely would have abandoned the nest earlier.

The second chick had remained at the scrape for at least 37 hours before wandering off the first time. Thereafter, it ran out and returned to the nest many times, as its older sibling had done earlier. On 10 December, at 08:00 hours, when the older sibling was 100 hours old and the younger 48 hours old, we recorded for the last time the similtaneous brooding of chicks in Nest 24. From that time, the older sibling did not return to the scrape, and only six hours later the younger sibling abandoned it. Thus, final abandonment by both chicks took place about the same time, despite the difference in their ages.

Soon after abandoning the nest, both chicks moved some five meters to the base of a small rock cairn built some time previously by humans. The cairn had served as one of several perches favored by the adults of Nest 24 since the predation of two tern nests (Nos. 22 and 23) there. Assuming that adults influence the movements of young through brooding, and possibly other behaviors, the attraction that the cairn had for these young birds was astounding. From 21:00 hours on 10 December, they remained at the base of the cairn. When not brooded or fed, they hid among the rocks. On the morning of 11 December, we moved the chicks together, and also one at a time, to a variety of places within 10 meters of the cairn. Invariably, they returned to the cairn despite obstacles of snow and stone, and even while the adults flew overhead protesting. When last checked at

20:15 hours on 11 December, both chicks were still at the base of the cairn. We had no opportunity to observe them further.

The feeding habits of the tiny chick were no less remarkable. In addition to thrusting its head upward while opening and closing its mouth, the newly hatched young begged for food by rubbing its tiny mandibles against the bill of the parent. Although we were not certain when the first successful feeding took place, food was brought to the nest soon after hatching of the first chick. An initial attempt at feeding was aborted when the brooding parent, after receiving a minnow from its mate, simply held it in its bill without attempting to pass it to the chick. Finally, the attending bird retrieved the minnow and flew off. The chick must initiate the feeding by first emerging or popping its head out from beneath the brooding parent. Failing to do so at the proper time resulted in a number of aborted feeding attempts.

The older chick appeared ravenously hungry when 11 hours old. We watched one of the parents fly in with food, probably krill, and place it directly in the chick's mouth without first passing it to the brooding mate. The chick had trouble handling the item before swallowing what may well have been its first meal. It quieted down immediately and remained still for about an hour before calling and pecking at the parent's bill again. Our first observed successful feeding of the younger chick occurred when it was only five hours old. With surprisingly little difficulty, it swallowed an entire minnow.

We did not record every feeding thereafter, but our record indicates that it was very irregular. At times, the parents did not deliver food for periods of 2.5 hours or more. Minnows, at least two kinds, were important food items, perhaps more so than krill. Adult terns occasionally fed in the inlet near the tern colony, and at times in the bay near Palmer Station, but most of the food brought in came from unknown sources.

While the chicks were still being brooded at the nest scrape, the adults fed the chicks either within or outside the scrape, depending largely on where the young were at the time the adult arrived with food. If one chick refused food, as sometimes happened, it was given to the other, or simply eaten by the adult. Four-day growth rates show a fairly steady increase in weight for the younger sibling, much less so for the older, although the birds were of different ages when weighed.

We observed carefully the early hatching at Nest 10 in order to make comparisons between it and Nest 24. The first chick at Nest 10 hatched at 04:00 hours on 8 December, followed about two days later by the second (02:30–05:00 hours on 10 December). Both chicks were in the scrape during each nest-check on 10 December. By the following day, however, the older chick wandered about and hid among the rocks. When 90 hours old, it weighed 33.8 gm.

Hatching at other nests took place from 8 December on. By 12 December, Nest 10 had two chicks, and Nests 11, 13, and 17 one chick and a pipped egg each. Hatching was about to take place at Nests 3, 14, 20A, 21, and 29. Hatching on Bonaparte Point probably peaked during 10–14 December. By including data from eggs (Nest 30) hatched in an incubator, the spread of hatching can be extrapolated and placed at 12 days (6–18 December).

Predation

Skuas are principal predators of Antarctic Tern nests. On Bonaparte Point, both South Polar Skua (*Catharacta maccormicki*) and Brown Skua (*C. lonnbergi*) contribute to what appears to be a complex hybrid population of skuas not studied to date. Until this population is better understood, we prefer to call the Bonaparte Point birds by the common name "skua."

Unusually large numbers of skuas occupying Bonaparte Point make reproduction more difficult for the terns. By 12 December, ten pairs of these skuas had nests and four additional pairs defended fresh scrapes or special areas. There also was a considerable non-breeding element of 30 or more skuas. No doubt the build-up resulted from an artificial food supply at Palmer Station where the birds are fed daily. These feedings also resulted in regular flights of skuas between Palmer Station and Bonaparte Point. The main body of nesting terns (Area A) was directly on a popular flight-line that ended near the glacier at a roosting ground containing as many as 39 skuas. The terns of Area A were up in the air chasing skuas much of the time, although not every incubating bird flew up each time a skua went by.

Time and again we noted that terns actively pursue flying skuas. Soon after a skua touches down, the attacks diminish both in frequency and intensity, often ceasing altogether, even at times when the predator lands fairly close to a nest. We also noted that a grounded skua does very little walking and searching.

On three different occasions, we saw a flying skua suddenly drop down beside a tern nest, eat the entire clutch, and fly off again without searching for other nests close by. And, according to our observations, the skua that sometimes lands a short distance from a nest does not always get the eggs.

Our overall record of predation also indicates that skuas do not hunt eggs while on the ground. Although the heaviest nest predation occurred where the terns were most concentrated (Areas A and B), there was no mass destruction or even the loss of several nests at a time. Of 21 nests under observation in Area A from 22 November to 12 December, seven (33 per cent) were destroyed by predators. Six of the seven nests were in the center of the colony where the birds were highly concentrated. Most significant was the time or spacing of predation: Nest 5 was destroyed on 27 November; Nest 12 on 28 November; Nest 7 on 29 November; Nest 19 on 1 December; Nest 8 on 6 December; Nest 9 on 7 December; Nest 33 on 8 December.

At Area B, where 11 nests were concentrated, predation was even greater (45 percent). Skuas also picked off these nests one at a time on different days: Nest 26 on 24 November; Nest 22 on 26 November; Nest 31 on 27 November; Nest 23 on 2 December; Nest 35 on 7 December (eggs replaced with those from abandoned Nest 28 and immediately accepted). The percentage of predation may have been greater if we ourselves had not removed the abandoned eggs of Nest 4 (Area A) on 30 November and of Nest 34 (Area B) on 7 December.

All nests (Nos. 20, 29, 30A, and 36) outside of Areas A and B had survived up to the time we left Anvers Island. In the beginning, we thought these isolated nests would be the first to go, since the one or two birds defending each of them would not be nearly as effective as a flock in driving

Antarctic Tern chicks. Painting by David F. Parmelee.

off marauding skuas. It would appear that factors other than sheer numbers of terns play a greater role in the survival of nests.

Most early nesting skuas occupied the main ridge of Bonaparte Point well apart from the nesting terns, whereas the main body of non-breeding skuas roosted near them. A few pairs of late-nesting skuas defended areas immediately adjacent to the terns. One pair of skuas, not far from Area A, completed its clutch on 8 December. Another situated between Areas A and B caused us so much concern with respect to nest predation that we decided to remove the predators on 1 December. Within 24 hours, another pair of skuas occupied the same ground.

Skuas defending nesting areas adjacent to penguin rookeries are thought to benefit the penguins in the long run by driving off excessive numbers of their own kind. Whether skuas benefit the terns in a similar way was not obvious to us; the point needs further study.

In addition to skuas, a number of Kelp Gulls (*Larus dominicanus*) and a smaller number of Giant Fulmars (*Macronectes giganteus*) breed on Bonaparte Point. Although these birds are potential predators of tern eggs and chicks, we found no evidence that they harmed or even bothered the terns very much. At times, the terns chased gulls but not nearly so often, or with the same ferocity, as they did skuas. The terns were prone to chase dark immature gulls more than adult gulls.

Thirty-nine gull nests were scattered on rocks at the glacier end of Bonaparte Point. Most had full clutches by 22 November. Nesting gulls virtually ringed Area A and nearly surrounded Area B. Two late-nesting gulls crowded the terns by building nests at the very edge of Area B. Another late-nesting gull there, unable to find a suitable rock, laid its eggs in a nest constructed entirely on deep snow. Eventually, the eggs dropped through the nest lining when the snow melted. It is evident that the areas defended by terns are also choice nesting sites for other birds.

With one notable exception, Giant Fulmars did not nest very close to the terns of Bonaparte Point. Tern Nest 30A, on the opposite side of the peninsula from Areas A and B, was within 20 meters of a cluster of seven Giant Fulmar nests. At no time did we see interaction between the two species.

At the Humble Island tern colony visited briefly on 25 November, we found Giant Fulmars incubating very close to active tern nests, in one case only three meters away. Although we saw no clearly defined boundary separating the two colonies, we had no opportunity to study interactions between the two species.

Survival

Our study of the terns of Bonaparte Point was too brief for a full appraisal of predation and survival; but this much we know. Of 37 nests observed from 22 November to 12 December, at least seven (19 percent) were doomed from the start in having single, unattended eggs. The remaining 30 nests held a total of 57 eggs, of which 34 (60 percent) survived either as live embryos or small chicks. Predators destroyed 18 (31 percent) of the 57 eggs; we were responsible, directly or indirectly, for the loss of five (8 percent). We witnessed no loss of small chicks through predation. The survival of 60 percent seemed remarkable to us, considering the large number of skuas and other predators at the breeding spots, not to mention our frequent interventions.

Our activities probably resulted in two nest desertions. We have no idea why Nest 4, with two well-incubated eggs, was deserted on 26 November. The pair at Nest 27 abandoned their two eggs with large embryos soon after we captured and marked one of the parents on 30 November. Placing the blind close to the nest too soon may have caused the desertion rather than the capturing and marking, for no other marked birds deserted nests. Once accustomed to the blind, the terns did not seem to mind it, although any noise made by us within the structure invariably caused alarm.

Probably the greatest threat to tern colonies with respect to human intrusion is the accidental stepping on eggs. We inadvertently stepped on Nest 1, destroying its single egg, at the very start of our study. Only with great care did we avoid duplicating the disaster.

An inexperienced person walking overland by way of exposed ridges to avoid the snow, could quickly devastate a tern colony. The Antarctic Tern is mild by comparison with the Arctic Tern, which tends to drive humans off through repeated vicious attacks. Although the former is noisy and certainly committed to swooping and dive-bombing, it seldom strikes hard, even while one handles its chicks. Known tern colonies near southern stations such as Palmer should be off-limits to all personnel except those cognizant of the breeding conditions.

Conclusions

In many ways the Antarctic Tern closely resembles others of the genus *Sterna*. Obvious likenesses are external morphological characteristics, such as the various young and adult plumages. Many aspects of its breeding biology, including clutch size, egg-laying, and incubation periods, are very similar to other *Sterna*. The behavior of the adults in colonizing, maintaining territories, and care of eggs and young is typically *Sterna;* but in adapting to conditions of the south polar environment, they show remarkable diversities.

Unlike other *Sterna,* the Antarctic Tern is essentially an early breeder even at high latitudes where conditions are least favorable. It is among the very first of the south polar species to breed.

The fact that so many of the far southern species and large numbers of individuals nest close together in restricted habitats within fairly extensive exposed areas leads one to suspect that there must be relatively few suitable areas available to most of these birds. It is logical to assume that a high priority is assigned to those areas that open up year after year in contrast to others subject to more severe climatic fluctuations. Whatever the reason, the fact remains that a few select areas support most birds, and this results in a scramble for choice nesting sites. Evidently, the advantages of nesting in the favored areas far outweigh the disadvantages of congestion. In order to compete successfully with other species, the terns arrive and claim their nesting grounds early each year. This may explain in part why they are so faithful to the traditional grounds, and why they even delay nesting for long periods when necessary.

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SOCIAL STRUCTURE AND REPRODUCTIVE BEHAVIOR IN THE GREATER RHEA

DONALD FRANCIS BRUNING

Photographs by the author

The Greater Rhea (*Rhea americana*) was first described as a new world "ostrich" (Piso, 1648; Marcgrave, 1648). *Rhea americana* is gray in color with body coverts ranging to white on the rump and thighs. A dark, nearly black, section of the neck and chest is usually more pronounced in the male, but is often visible on some females. These birds may stand one hundred and fifty centimeters tall and weigh up to forty kilograms (Austin and Singer, 1961; Bruning, 1973). This rhea is predominantly an inhabitant of the vast pampas grasslands of Argentina; however, its range extends south to the fringes of the semi-arid scrubland hills of Patagonia and north to the edge of the semi-tropical marshlands of Brazil (Hellmayr and Conover, 1942; Peters, 1931).

Very little was known about the habits of these flightless birds until the ornithological surveys of Hudson (1920) and Wetmore (1926) gave some behavioral accounts. Both before and after these surveys nearly all accounts of rheas have been related to their maintenance in captivity. Rheas were reared in captivity as early as the mid-1800's by Schmidt (1886). Rearing and maintenance techniques varied with each investigator and no two even used the same diet. As a consequence, the results varied as greatly as the methods, until detailed scientific accounts finally started to appear with the work of Junker (1950), Steinbacher (1951), and Veselovsky (1953, 1956). This trend of scientific accounts culminated with Faust (1960) who at the same time recorded a few notes on rhea behavior. Still there were no detailed accounts of rhea behavior until Raikow (1968, 1969) described the behavior of captive birds. Raikow's work was very limited in its detail of reproductive behavior, and there still exists no complete description of rhea sexual behavior either in captivity or in the wild. This report will attempt to describe in some detail the reproductive behavior of the Greater Rhea under both wild and captive conditions. Male behavior is emphasized to demonstrate its relationship to this unique social system in which the roles of the sexes are reversed during incubation and rearing of the young.

Methods

This study began in January 1968 with a captive flock of seven Greater Rheas at the New York Zoological Park.

Over a four-year period, captive birds were observed in four enclosures.

Field observations were made on the estancia "El Callejon" near the town of Castelli in Buenos Aires province, Argentina during November and December of 1970, and October and November, 1972.

This area is a low, nearly flat flood-plain about 200 meters from the bank of the Rio Salado. The major vegetation of the area is grass and clover with patches of other herbs.

The climate in this part of Argentina is dry temperate with summer maximum temperatures over 38° C and winter minimum temperatures around 0–1° C. Frost occurs only a few times each winter. The climate is quite moderate due to the area's proximity to the South Atlantic, less than twenty kilometers away.

In Argentina, Greater Rheas could not be approached on foot but were observed with binoculars from between 20 meters and one half km away. Blinds were not feasible due to the movement of the rheas and the vast area to be covered. Remaining inside a truck proved to be the most successful way of observing rheas.

I observed captive rheas from one to more than eight hours every day during the breeding season. In Argentina I spent eight to 12 hours daily in the field recording observations on rheas.

Captive individuals were identified by colored leg bands or by individual characteristics, such as a large callus on the right leg, etc. In the wild, identification was possible only for males with nests and for groups of females by location.

Social Structure: Non-Breeding Season

The Greater Rhea is gregarious during the non-breeding winter season. Flocks of 15 to 40 birds were commonly observed during my study but Hudson (1920) and Wetmore (1926) reported flocks of up to 70 birds. Although I did not study wild birds during the non-breeding season, native ranchers and gauchos whom I questioned indicated that all rheas, except for a few solitary males, gather together in flocks of one hundred or more birds during the winter months.

In captivity, most aggression stopped during the non-breeding period, except for the maintenance of individual distance. All members of a flock of rheas intermingled with relative freedom even though a definite peck-order existed within the flock. The dominant males retained their dominant positions throughout the year. Aggressive encounters during the non-breeding season were very mild in comparison with those that occurred during the breeding season. All except two of the 122 encounters observed consisted of a simple threat (to be described later) which resulted in the retreat of the threatened bird. Two encounters involved a short chase by the dominant male when approached by another male while feeding. Only 16 of the encounters occurred when a resting bird was disturbed. All other encounters occurred either at a food container or while birds were looking to be fed by zoo visitors along the enclosure fences.

Eighty percent of the aggressive encounters during the non-breeding season occurred between males and less than 10 percent between females. Male 1 dominated 74 of the 122 encounters; Male 2 was dominant in 23 encounters. Females were aggressive in 11 encounters, and only once was a female dominant to a male (Male 4). These figures indicate that the peck-order was male dominated.

Social System: Breeding Season

With the first warm days of late winter and early spring in the southern hemisphere, the large flocks of Greater Rheas start breaking up. Adult males are the first to leave as aggression increases (E. Barreto, pers. commun.).

Among captive rheas, the most dominant male tended to drive out other males that had become reproductively mature. Although the situation among wild birds is not known, Hudson (1920: 233) states that "The young males in the flock are attacked and driven off by the old cock-bird; and when there are two old males they fight for the hens."

In Argentina, as spring approached, the flocks began splitting so that by the onset of the breeding season the social structure consisted of three components (Table 1): single males, small groups of females (2 to 15) with one or two males, and larger flocks of yearlings (up to 40) with some non-breeding adults. These may be two-year-olds, as Hudson (1920) suggests that breeding does not occur until the third year. In captivity, rheas can breed at just over one year of age; however, captive birds generally breed in their second year (Bruning, 1973b).

From March to September the Greater Rheas gathered in flocks of ten to one hundred birds with only a few isolated males (E. Barreto, pers.

TABLE 1

Size of Flocks of Rheas Observed in Argentina
(November 1970 and October 1972)

Adults		*Juveniles*	
Number in flock	*Number of flocks*	*Number in flock*	*Number of flocks*
2	2	6	1
3	5	12	1
4	5	14	2
5	4 (1)[1]	21	1
6	14 (1)	22	1
7	4	26	2
8	8[2] (2)	30	1
9	5		
10	2 (2)		
11	2[3]		
12	2		
13	1		
14	3 (1)		

Individuals, other than nesting males, observed singly: 117 males, 7 females.

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[1] Figures in parentheses indicate number of additional flocks with two males. All other flocks had one male each.

[2] One additional male seen near one flock.

[3] Two additional males seen near one flock.

commun.). From September to February, single males and small groups are the general rule (E. Barreto, pers. commun.).

Captive Rheas

By the onset of the breeding season, the dominant male had driven all other males out of the wintering flock and actively displayed for females. All other males were solitary and avoided the females when accompanied by the dominant male. The relatively small enclosures led to frequent — if not almost continuous — aggressive encounters (Table 2 and Figure 1).

During the height of the breeding season, over 99 percent of all aggressive encounters were between males, with nearly 70 percent involving the dominant male. However, once the dominant male began incubating a nest of eggs, the number two male assumed the dominant position in aggressive encounters with males lower in the hierarchy (Table 1).

At the New York Zoological Park, male rheas became aggressive and even began courtship display as early as September and October on warm days (Figure 1). However, the cold winter weather seemed to delay completion of the male reproductive cycle. Courtship display and aggression began to build up anew on each warm winter day. Since the females did not produce eggs until early spring, it remains unclear whether they required more warm weather and/or a longer photoperiod for the initiation of their own cycle, or whether their reproductive state depends on the intensity of the males' display.

Wild Rheas

In Argentina, the Greater Rhea started producing eggs by the end of September or early October. The question still remains as to whether the males in the wild also engaged in courtship on warm days during the winter or whether this behavior in captive birds was due to the fact that their biological clocks did not fully reset for the northern hemisphere.

On the Argentine pampas, the flocks of females and yearlings started breaking up in July or August (E. Barreto, pers. commun.). By late Sep-

TABLE 2

Aggressive Encounters Between Males Under Captive Conditions During the Breeding Seasons of 1970 and 1971

Aggressive rhea	*Recipient of aggression*	*Total number of encounters*	*Number of chases*	*Number of fights*	*Number of threats*
Male 1	Male 2	368	182	14	172
Male 1	Male 3	243	62	1	180
Male 1	Male 4	139	6	0	133
Male 2	Male 3	210	33	2	175
Male 2	Male 4	65	2	0	63
Male 3	Male 4	14	3	0	11
Male 3	Male 2	12	1	0	11

tember or early October, the adult females split up into small groups, usually six to eight but ranging from 2 to 15 birds (Table 1). These small female flocks then became the harems for which males competed. Flocks contained one male and two to 15 females. A male and his harem remained together in a relatively stable social bond. Occasionally, when two groups came together, one female switched from one flock to another as they separated. Under these circumstances, a female usually switched to the group whose male was displaying more vigorously. Transferring also occurred regularly when the very dominant male of one flock challenged or chased the male of the second group. I observed this six times in October 1972, but only once did the two groups consolidate. On the other five occasions at least one or two females did not join the larger harem of the dominant male, but remained with their subordinate male.

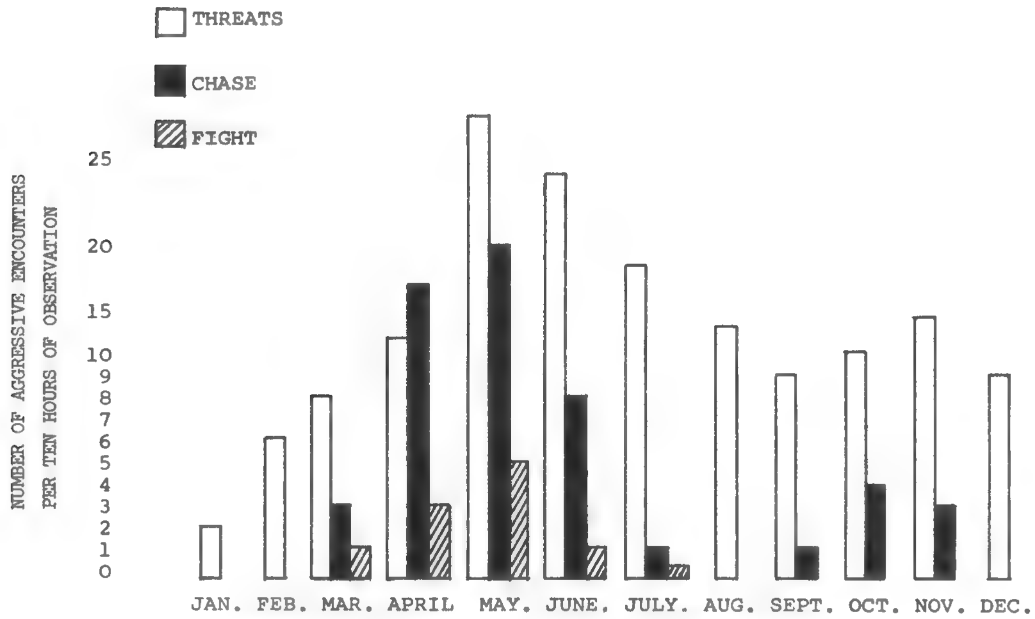
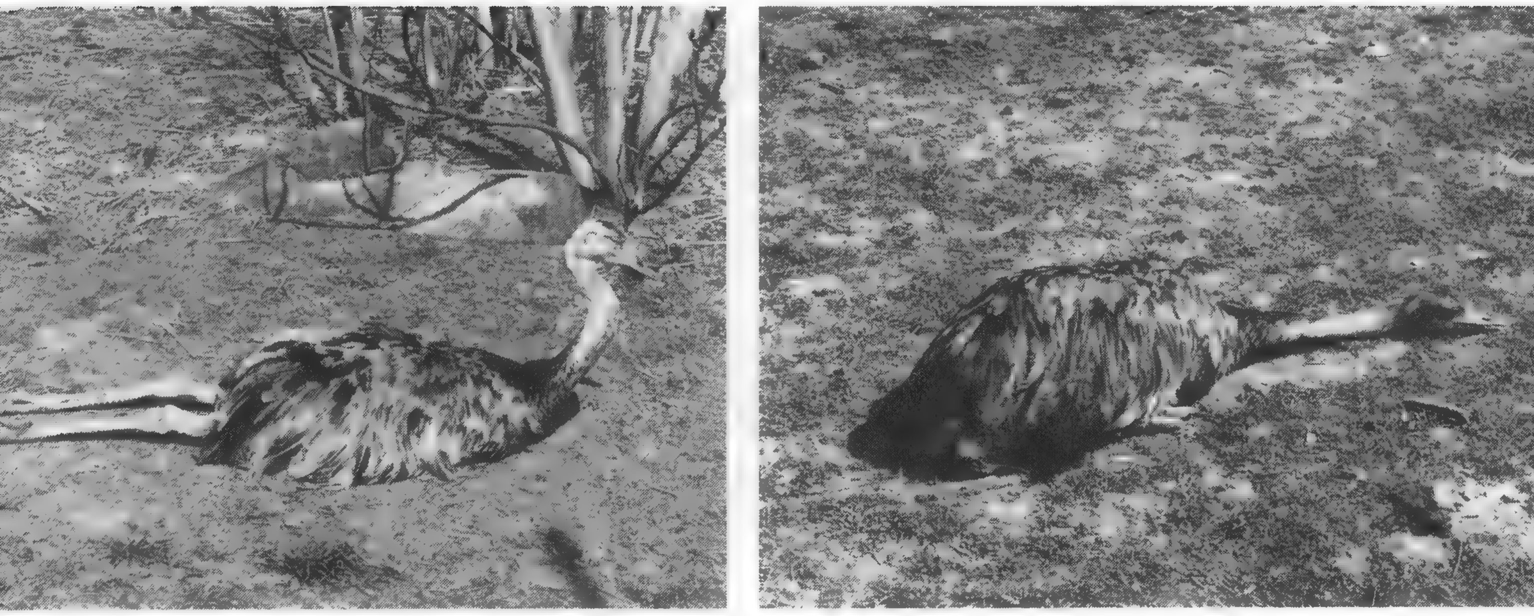


Figure 1. Frequency of aggressive encounters among captive rheas in 1971.

Yearling birds, as well as non-breeding adults, remained in their own flocks of up to 50 individuals even during the breeding season. In the wild, young birds do not reach adult size or sexual maturity until at least two years of age. Sexual maturity is characterized by defiant posturing, aggressive behavior, darker coloring, and erected head and neck feathers. Young females or adult females that attained a readiness to breed more slowly joined harem flocks randomly when their flock approached a male and his harem. Seldom did I see adult females alone, which indicates that they join harems as soon as they leave the juvenile flocks.

At the onset of the breeding season, wild rheas occur in three easily observable social groupings (Table 1): (1) females with one or more males, (2) single males driven out of flocks by more dominant males, and (3) yearlings and non-breeders. These three social groups remained intact throughout the breeding season. A fourth grouping emerged later in the breeding season when a male and his chicks maintained social bonds as a family through the summer and into the following winter. These family groups and yearling flocks were the nucleus for the large wintering flocks.



Figures 2 and 3. Two positions assumed by sleeping rheas.

Agonistic Behavior

Individual Distance

Even though rheas gather in flocks throughout the year (Table 1) and spend most of their lives in some type of social group, they defend a zone around themselves into which other rheas are not allowed except during certain courtship and nesting activities. This individual distance (Raikow, 1968) is maintained by the less dominant birds avoiding contact with more dominant birds by simply moving away from them — in captivity, when the rheas cluster around a food pan or along a fenced enclosure.

The individual distance increased to an area several meters in all directions when a rhea sat down. Its diameter increased with age, seemed to decrease for females during the breeding season, and was greater for males, especially when they excluded other males during the breeding season (Table 3).

Head-forward Threat Display

Any time a rhea violated this individual distance, one or both parties threatened the other with what Raikow (1968) termed the "head-forward threat display." This display consists of intention movements of biting. The neck is drawn back into an S-shaped curve and a hissing sound is emitted through gaped bill.

When an intruder approached to within seven meters of a resting bird, the latter became alert and remained so until the trespasser came within three to five meters; the resting male gaped, withdrew the neck into an S-shape (Figure 4) and faced the interloper. Any further approach brought a head thrust toward the advancing bird with bill agape and accompanied by a loud hissing. Sham-biting occurred at the end of each thrust. The male rhea withdrew his neck into the S-shape after each strike and repeated the thrust again and again. If these threats did not intimidate the intruder, the resting bird assumed a crouching position or stood up, at which point all belligerence ceased unless the intruder continued to move closer. The defending bird then usually preened and moved away slowly.

Dominant males, of course, did not move away when approached by another rhea, but remained stationary and threatened the intruder (Tables 1 and 2). During well over one thousand hours spent watching rheas both in nature and in captivity, not once did a dominant male move away when disturbed by another rhea.

The Head-forward Threat Display was the most common threat behavior. The bill-gaping and head-thrusts seemed to be ritualized acts of biting, while the hissing probably enhances intimidation. Spurway and Haldane (1953) consider hissing to be an exaggerated expiration sound. Raikow (1968) looked upon gaping and thrusting as intention movements of biting. The level of motivation determined the frequency of this threat display as well as its components. Gaping occurred under low motivation, and head withdrawal and thrusting occurred more and more rapidly as motivation increased. This Head-forward Threat Display was most intense in a male defending his nest of eggs; however, it occurred to a lesser extent in any rhea sitting on the ground. A standing rhea usually moved away when disturbed unless he was the dominant male.

The typical threat posture of a standing male consisted of lowering the front of the body with the neck held in a low U-shaped loop with bill agape. The threatening male then slowly took a few steps toward the other male. If the intruder did not depart at the first sign of the dominant male's threat, a chase usually took place. Chases were never directed at a female (Figures 4 and 5).

TABLE 3

Occurrence of Observed Threats[1] Made by Breeding Male in Argentina During October 1972

Situation	*Number of threats*	*Proximity of intruder before threat was elicited*		
		Over 20 m	*10–20 m*	*1–10 m*
Single bird sitting	45		41 males[2]	2 males
Single bird standing	39	16 males	23 males	
Single bird lying[3]	54		52 males	2 males
Sitting on nest	87		74 males	10 males 3 females
With group of females	183	163 males	20 males	
Total	408			

[1] Threats only; this does not include fights or chases during more than 100 hours of observation. Sixteen fights and 123 chases were observed.

[2] Object of threat.

[3] Lying means that the bird had head and neck stretched out on the ground when disturbed (Figures 2 and 3).

Attack Behavior

A dominant male rhea usually threatened another male and slowly took a few steps toward him before breaking into a full charge. The subordinate male, running to escape, maintained a submissive posture by holding his head and neck low and drawn back into an S-shape or outstretched nearly horizontal. The pursuer ran with his head and neck in the same S-shaped curve, but continually tried to strike his adversary with thrusts and bill snapping. Nearly all biting or striking attempts were aimed at the opponent's head, neck, and back. The pursuer raised his wings over his back as he ran.

Portielje (1925) described a defense posture in which rheas held the neck upright and did not flutter the wings. It was Raikow's (1968) contention that this occurred only under low motivation. In my study, I observed similar behavior only under captive conditions in which one male was dominant to the extent that subordinate males made no attempt to challenge the dominant bird or to display unless the dominant male was out of sight. In Argentina during October 1972, I observed a total of 123 chases involving only males. Only five chases lasted more than 30 seconds and 95 lasted less than 10 seconds, indicating that most chases are largely intimidations between males.

Actual combat seemed to be confined to dominant males early in the breeding season. I never observed physical combat involving a female. In Argentina, I recorded fights either between a male with females and a single male, or between two males with groups of females. A total of 16 fights averaged 64 seconds. They seemed to occur more frequently early in the breeding season and most frequently involved two equally, or nearly equally, dominant males. The fact that all fights involved at least one male possessing a harem seemed to imply that fights were for the acquisition or retention of the females (Figure 1).

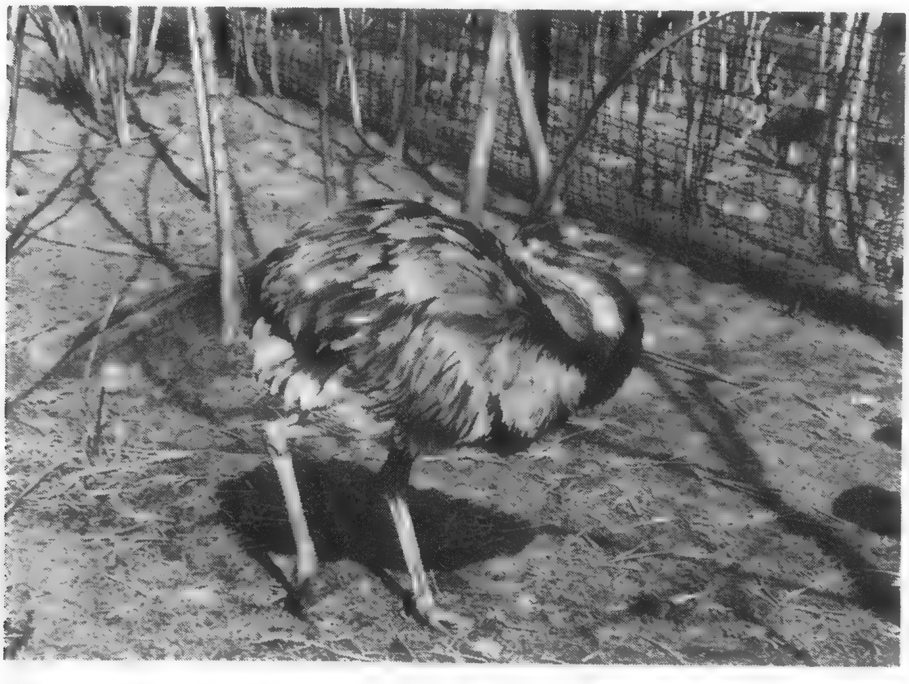


Figure 4. A captive male rhea in a threatening display.

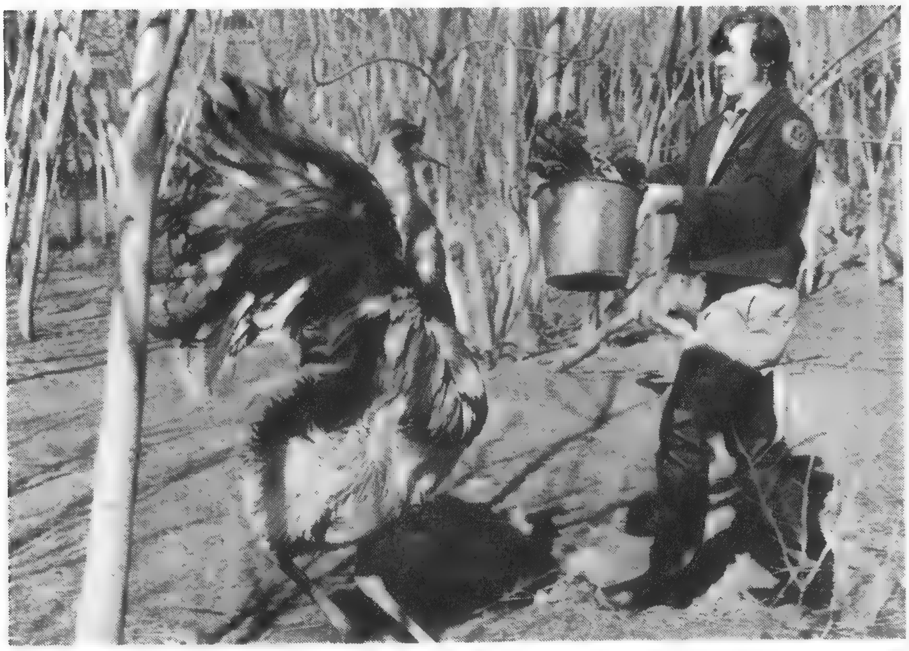


Figure 5. A male rhea attacking the keeper.

Combat occurred much more frequently in captivity when dominance positions were being determined early in the spring before harem flocks had formed. A male with a harem had a great advantage over any intruding male and usually drove him away. Even if a physical conflict occurred, the male successfully defended his harem in over 90 percent of the 43 conflicts observed.

Escape

When alarmed or pursued, rheas fled using an evasive zigzag path. The wings in the folded position were raised high over the back forming a tent-like triangle as the bird ran away. The closer the pursuit the higher the wings were raised. As the pursuit got closer the rhea used very evasive running tactics. A zigzig path was extremely evasive alone, but the rhea also used the wings to confuse the pursuer. When the rhea made a sudden turn while running, the wing on the side opposite the direction of the turn opened and gave the illusion that the bird was continuing along a straight path for a second. Then the wing was drawn back with a sudden jerk as the rhea headed in a different direction. The nature of the pursuer did not affect this behavior since I saw it every time a rhea was closely pursued (within 30 meters) by another male rhea or by man, whether on foot, horseback, or in a car.

Raikow (1968) states that the pursued bird held his wings either high over his back or spread laterally. However, I noted that a subordinate male held his wings high over his back only if he was some distance from the dominant male. Even then, the high position of the wings was likely to provoke further attack. When the subordinate bird was pursued closely, he slowly lowered his wings and held them laterally while flicking them up and down slightly at a rapid, but sporadic, rate. This wing flicking seemed to be a submissive signal, since females also used it when approaching a male's nest. During a chase, the escaping male made evasive zigzig maneuvers whenever the pursuit was at all close.

With the wings in a slightly raised position and with sudden turns and flicks of the wings, a white rump was exposed. From a distance, the white flashes of a fleeing rhea probably act as an intraspecific escape releaser. In 24 of 26 chases observed in Argentina in October 1972, other rheas joined in flight. On the two occasions, no other rheas were within 400 or 500 meters of the disturbance.

A male also used the raised wing position when attacking another rhea, and the head and neck were held in a tightly compressed S-shape ready for the snake-like strike. During the mating season this attack was directed only at males; however, a male with chicks up to one week old attacked any rhea that approached. Captive rheas violently attacked anything that approached within seven meters of the male and chicks during the first two days. They tolerated other rheas closer with each passing day.

Wing Position

The height of the wings varied from one fleeing individual to another and depended on the proximity and nature of the pursuer. The wings were held higher if the pursuer was close behind or if the chase was prolonged.

Observations of 103 aggressive encounters between males showed that the pursuer held his wings much higher than the pursued, and the pursued assumed a submissive posture during, or after, a chase to prevent the dominant male from persisting in the attack. If the subordinate male lowered his head and wings and compressed the feathers on his head and neck, the dominant male frequently discontinued the attack. No further attacks occurred if the subordinate bird remained over 100 meters from the attacker and his females.

Ninety-six of the 103 males driven away continued to move off to another area. Seven of the males continued following the dominant male and his females. All but one of these seven straggled along after the flock at distances varying from approximately 30 meters to over 100 meters. These six remained just far enough away so that the harem male would not attack them; and at the first threatening signs they retreated to a safer distance.

The one exception was a persistent male that continued to move in on a harem of eight females. After three fights and seven chases, this male was still trying to move in when heavy rain and darkness prevented further observation.

Courtship Behavior

Aggressive encounters and the defiant stance of adult males marked the approaching breeding season. The feathers of the head and neck fluffed out, indicating rising levels of sex hormones. This feather erection slowly extended to other areas, including the base of the neck, the breast, the thighs, the back, and finally the rump during the first week of the breeding season (Figures 6 and 7).

Call Display

The Call Display was the first actual display of the courtship period performed by the male with the onset of the breeding season. This display occurred with the first aggressive encounters in the spring and continued

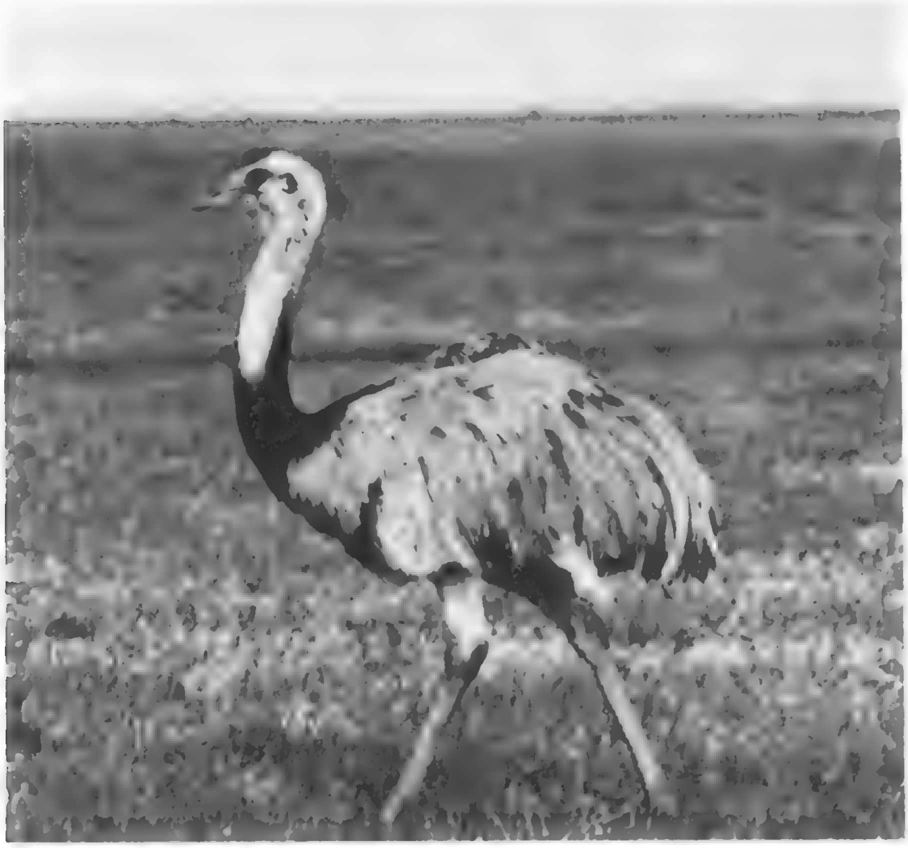


Figure 6. A dominant male rhea showing a defiant posture with ruffled head and neck plumage.

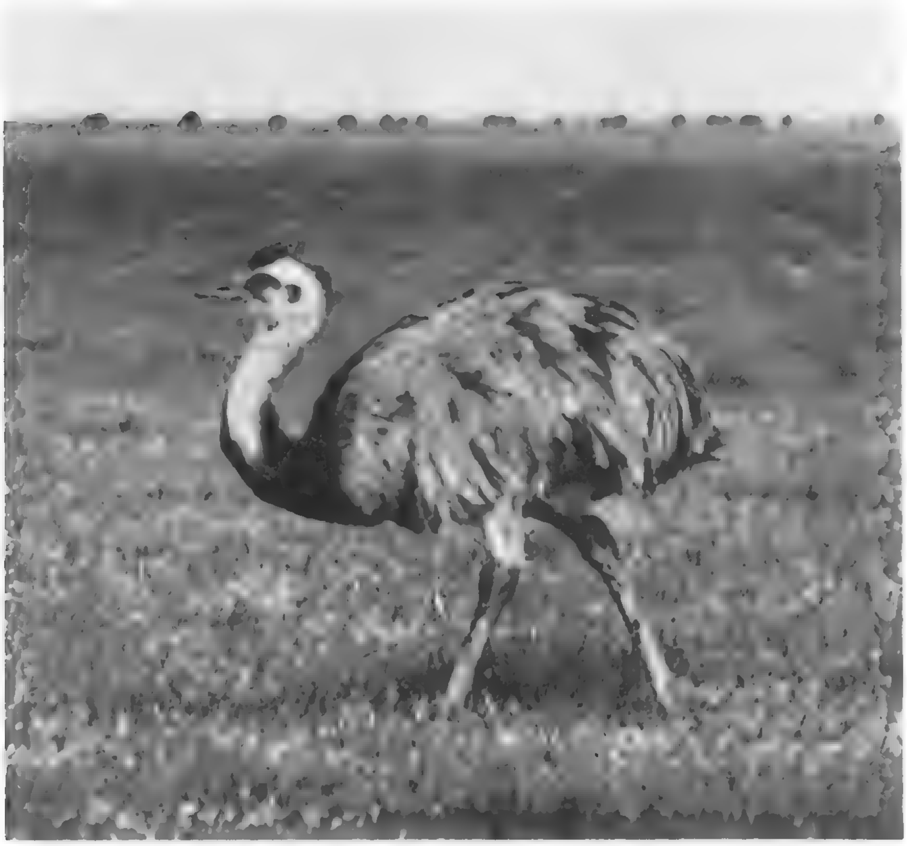


Figure 7. A dominant male rhea in a threatening posture as he approaches another male.

until a harem was attracted, courted, and defended; and mating had occurred. The display itself has been described by Raikow (1968) as follows:

> "The anterior end of the body is raised upward. The neck is held stiffly upward and forward, with the plumage ruffled to a maximum degree. The wings may be raised higher than before and the base of the neck is expanded. The call is then given, sometimes immediately and sometimes after a pause of several seconds. The call is deep-toned, with two notes, and lasts about one second. The first note is the deeper of the two, and falls in pitch, while the second note rises slightly higher than the first."

The call of the male rhea, although described in many different ways, is a very low sound that carries for great distances. After calling once or twice the male either relaxed or broke into a run. If subordinate males were present, the running often turned into a chase. The male frequently ran toward a female, which ran off with the male following. If the chase involved a female, the male assumed a less aggressive stance.

The call may attract the female's attention, as Raikow (1968) suggested; however, the fact that females showed no reaction to the call itself seems to indicate a minimal effect. The establishment or maintenance of a male's dominance could be a significant function of the Call Display; it seemed to be used frequently as a threat or challenge as well as a victory signal after a male had successfully driven off a challenger and retained his group of females. The fact that the Call Display, often referred to as booming, occurred much more often while males were establishing dominance seems to further support this view (Figure 8). Once a male had won a harem, he used the Call Display only as a threat or as a victory signal after another male had retreated. Booming did not seem to be part of the actual courtship display, as calling seldom occurred during courtship; however, its influence on harem formation or acquisition remains unclear.

The Call Display of the male rhea is definitely agonistic in nature and is so frequent during the early stages of courtship that it seems appropriate to consider it at least a preliminary part of courtship.

Wing Display

Once a male had established his dominance and taken over a harem, he had to defend his females and display to maintain the bond. Females wandered about feeding all day, and initially ignored the male, as he followed his harem and intensified his display.

The major courtship behavior consisted of Wing Display (Figure 9), during which the male lowered his head, spread his wings, and slowly walked toward the females, who at first seemed to ignore the advances and moved away feeding as he approached. The Wing Display has been described by Raikow (1968) as follows:

> "In the Wing Display the male slowly approaches the female, lowers his neck in a low loop, and walks beside her, sometimes bobbing his head slightly. The plumage of his head and upper neck is ruffled. This may continue for several moments while both birds peck and nibble at objects on the ground. Finally the male spreads his wings and walks beside or ahead of the female in full display with the anterior end of the body lowered slightly and the neck in a low U-curve. The wings are extended laterally and slightly forward, at about right angles to the longitudinal axis of the body. The humerus extends out from the body and droops slightly, the radio-ulna is directed vertically downward, and the manus is extended outward and down at about a forty-five degree angle. Often the wings are held so low that the plumes drag on the ground."

This display continued from 10 or 15 seconds up to 10 minutes. As the intensity rose, the male displayed longer, maintained postures more stiffly, and bobbed the head with more exaggerated movements.

As the frequency and intensity of this display increased the females began to stand around rather than move off as the male approached. His head slowly started swaying from side to side and up and down in a figure eight pattern. The females finally congregated around the male as his display intensified. At this point the male displayed with spread wings and now held his head low, swaying it in a horizontal figure eight pattern. The females, who gathered in a semicircle around the displaying male, began to follow the male when he moved off to feed between displays. As the intensity of the display continued to rise, the females stood in front of the displaying male for several minutes before they resumed feeding. A female, aroused by the male's display, approached the male with head held low and wings jerking slightly in a typically submissive manner.

The frequency of display increased greatly as the females responded. When a male acquired his harem, he displayed to them only three or four times the first day. By the eighth day the male displayed as frequently as five to ten times per hour during the day (Figures 10 and 11). The difference in display time between captive birds and those in nature (Figure 10) was probably due to the amount of time required for feeding. In a wild popula-

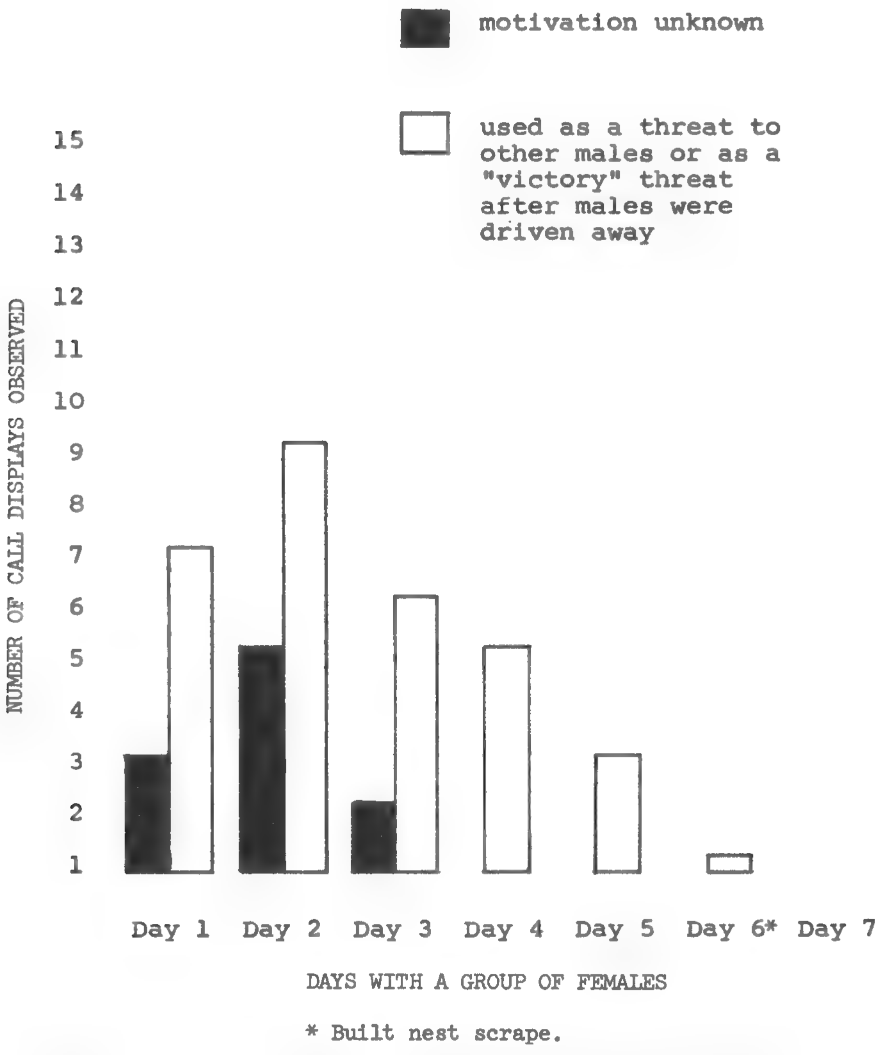


Figure 8. The frequency of one male's call display during the breeding cycle.

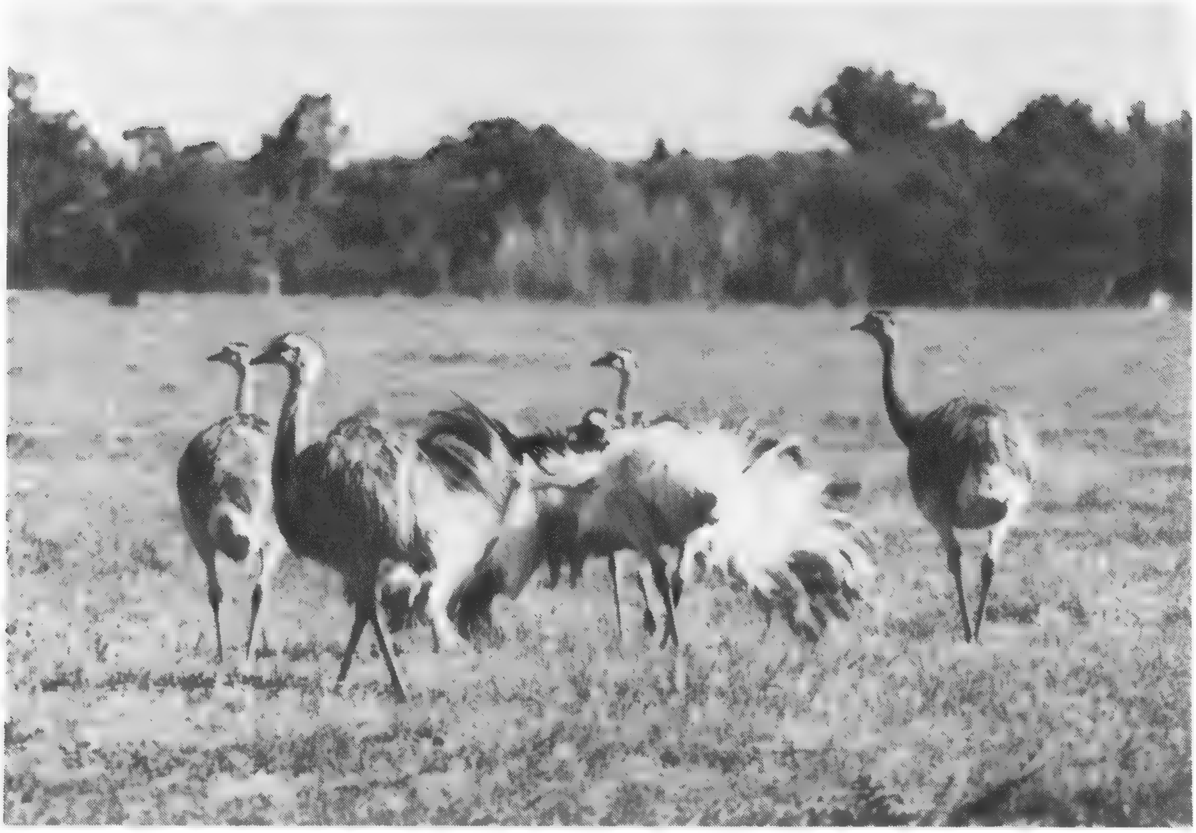


Figure 9. Male giving a Wing Display as females start to gather around him.

tion, the combination of feeding and display occupied over 95 percent of an adult male's time during the breeding season. Captive males with an abundance of food supplied at all times spent only a few minutes each day feeding, and as a result spent much more time displaying.

Raikow (1968) described a separate "Head-bobbing Display" as a precopulatory behavior given only to females sitting on the ground while the male was preparing, or attempting, to copulate. My observations of both captive and wild rheas suggest that head-bobbing is simply the final or most highly motivated part of the Wing Display. The extent and intensity of head-bobbing varied from male to male but most of all with the intensity of the display. The amount of head-bobbing increased with each Wing Display until finally successful copulation occurred. A sitting female stimulated the male to give a more intense display, which meant more head-bobbing. All of these observations point out that head-bobbing and swaying first started as a male approached a female during his Wing Display. Then as the intensity of the display increased and the females began to respond, the amount of head movement increased rapidly until it became the dominant precopulatory part of the display.

While displaying, males frequently attempted to grasp the feathers on a female's neck or back. The female usually pulled away from the male unless she was reproductively ready for copulation, in which case she sat down in front of the male.

Raikow (1968) suggested that the Wing Display probably evolved from the ritualization of displacement activities arising from approach-avoidance conflict, and that the wing spreading associated with this display is a ritualization of normal wing-preening activities. Wing-preening frequently occurred as a displacement activity at the end of a male's display if all females responded negatively and the male was unable to attempt copulation.

Morris (1956) suggested that ruffling of the plumage represents a ritualization of the autonomic pilomotor response to excitement.

Copulation

Periodically, one female remained beside a displaying male as the rest of the harem moved away, feeding. This female solicited by sitting until the male moved toward her and mounted. The female lay flat on the ground as the male grasped the feathers on the back of her neck with his bill. The male usually rested on his tarsi while copulating, but sometimes rested his body directly on top of the female. Portielje (1925) noted that the female lay flat on the ground with neck outstretched during copulation, while the male sat on his heels behind her making violent thrusting motions and holding the feathers of her neck with his bill. I observed a total of 16 copulations in captivity and 14 in the wild, each one averaging one-and-one-half minutes. Brito (1949) gives a two-minute average. The 14 copulations observed in Argentina lasted from 40 to 140 seconds. In one flock of seven females, the time between five copulations was 48, 60, 70, and 180 minutes.

After copulation, the male released his hold on the female's neck feathers and stood up, preened for a variable period, and moved off slowly

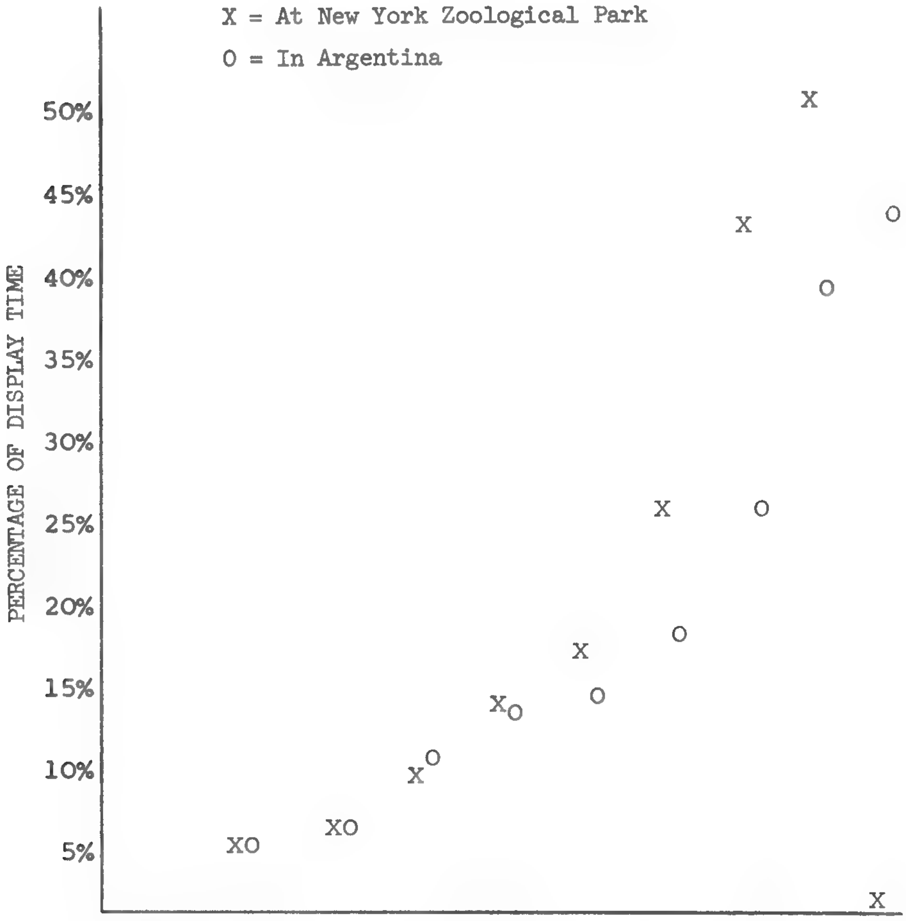


Figure 10. The average percentage of time that four males (two in captivity and two in Argentina) spent in epigamic display.

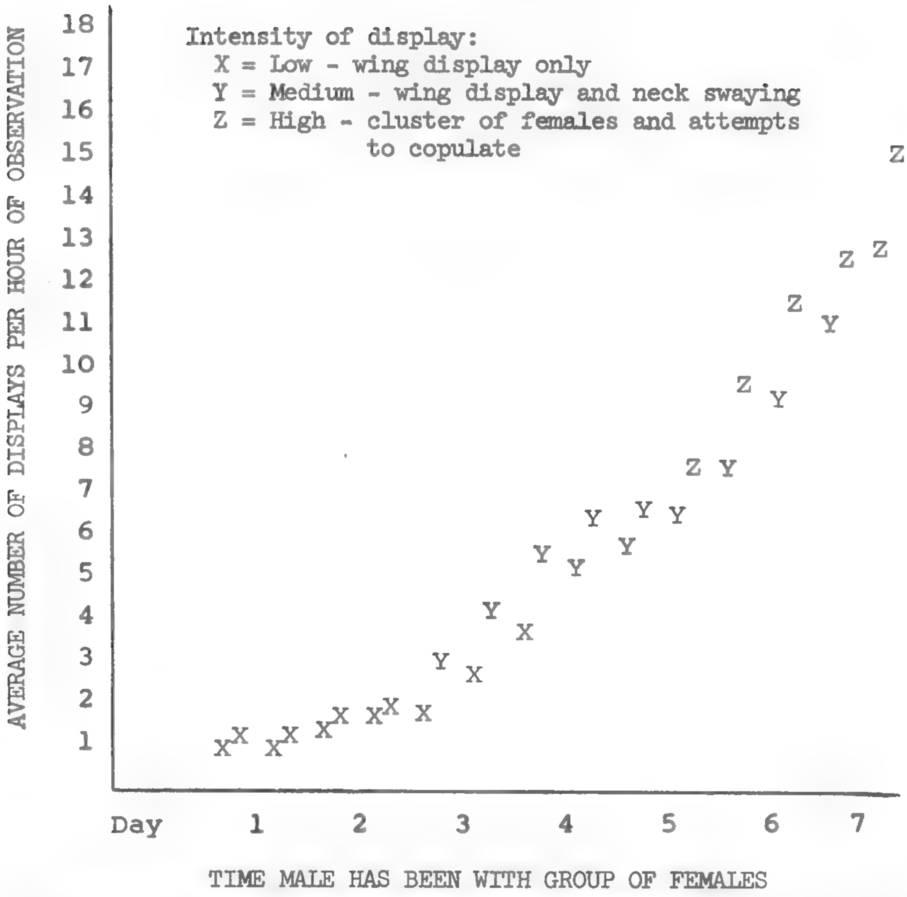


Figure 11. The average increase in the intensity of courtship display of three males at the New York Zoological Park.

toward the rest of his flock. Twenty to thirty minutes elapsed before the male displayed again.

The female often remained lying on the ground for several minutes before rising, preening, and moving off toward the rest of the flock. By separating three laying females from males at the New York Zoological Park, it was possible to establish that spermatozoa remained viable in the oviduct for at least one week. All three females continued to lay fertile eggs every other day for eight, five, and six days respectively after being separated from males. After these periods, one female continued to lay infertile eggs while the other two simply stopped laying. Since I did not know at what point the females had copulated before separating them from the males, it was not possible to determine how long sperm could be stored beyond the period of separation — at least eight days.

During the field study, I could not ascertain whether males mate with one female more than once in each breeding cycle. Under captive conditions, males definitely mated with one female on several occasions; however, I never observed matings with the same female within a one-week period. In Argentina, one closely observed male with seven females mated five times within two days.

Nest-building

After a period of displaying, the females start to follow the male continuously (Figure 12). The male eventually leads his harem to a possible nest site. This usually occurs around midday when rheas generally stop feeding and rest on the ground. These rest periods lasted for an hour or two during the hottest part of the day. While the females rested, the male searched for a suitable nest location. The male then trampled down all vegetation within a diameter of one to two meters. Measurements of 87 nests averaged 1.4 meters. The male then sat in the center of this area and performed in a manner similar to what Lorenz (1938) called the "hollowing movement" for Greylag Geese (*Anser anser*) — a movement that consisted of alternating backward motions of the feet that pushed soil and vegetation to the posterior edge of the nest scrape. Since the male kept turning slowly, a ridge of material was pushed up on all sides of the nest as he created a depression. Intermittently during the "hollowing movements," and after a scrape was made, the rhea pulled clumps of grass and dirt with his bill and threw them over his shoulder and back. Any sticks, stems, or other objects within reach of the bill were used in this way to build up the sides of the nest. The resulting depression was a nest scrape up to a foot deep. If the nest was deep, some of the tossed grass formed a lining for the nest. The final result was a depression in the ground lined with grass and edged with mounds of sticks, stems, and grass clumps all covered with pulled grass (Figure 13). The male continued to add grass or vegetation to the edges of the nest as he performed this "throwing over the shoulder" behavior each time he returned to the nest and after he rolled each egg into the nest.

Many males, under both wild and zoo conditions, built several nests. Sometimes several abandoned ones even contained a few eggs (Tables 4 and 5). Until the females started laying eggs, the male did not remain at any

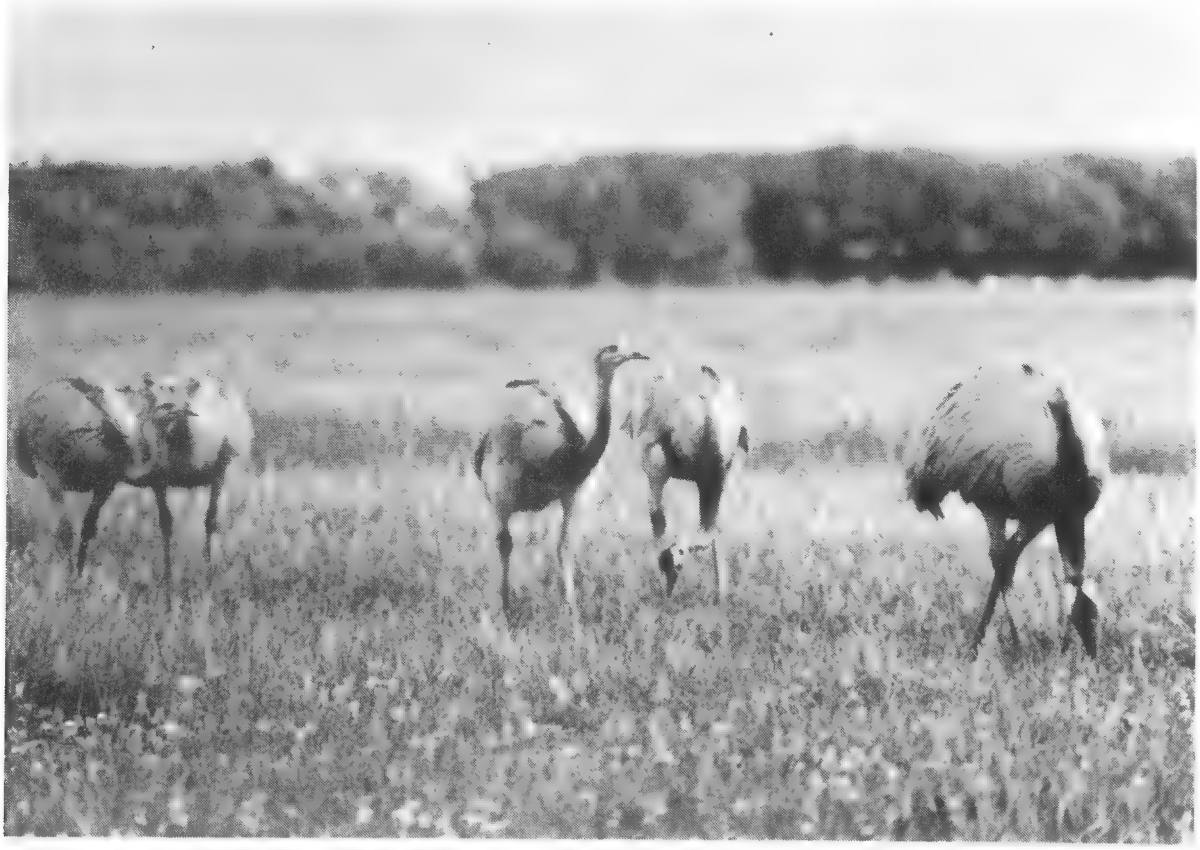


Figure 12. A group of four females following a dominant male as he leads them to his nest site.

TABLE 4

Nests of Greater Rheas Observed 15, 16, and 17 November 1970 In Buenos Aires Province, Argentina

Nest number	*Clutch size*	*Age of eggs*[1]	*Location of nest*	*Fate of nest*
1	23	I	S	Unknown
2	35	WI	T	Unknown
3	23	WI	T	15 hatched 18 November
4	27	WI	S	9 hatched 21 November
5	8	I	S	Broken and abandoned
6	51	I	T	Unknown
7	27	I	T	Unknown
8	21	I	S	Abandoned
9	3*	F	S	Abandoned
10	17	I	T	Abandoned
11	27	WI	T	22 hatched 28 November
12	5*	F	S	Unknown
13	4*	F	S	Abandoned
14	28	WI	S	Unknown
15	37	WI	S	Abandoned
16	1*	F	T	Unknown
17	5*	F	T	Abandoned
18	12*	F	T	Unknown
19	14	I	T	Unknown
20	4*	F	T	Unknown
21	62	WI	S	Abandoned
22	16	I	S	Unknown
23	14	I	S	Unknown
24	26	WI	T	18 hatched 29 November
25	3*	F	T	Abandoned
26	13*	F	T	Unknown
27	37	I	S	Abandoned
28	48	I	S	Abandoned
29	6*	F	T	Unknown
30	6*	F	S	Abandoned
31	16	I	T	10 hatched 30 November
32	3*	F	S	Abandoned
33	3*	F	T	Unknown
34	2*	F	T	Unknown
35	Unknown			20 hatched 20 November
36	Unknown			5 hatched 26 November

Average clutch size of all nests: 18.7 eggs.

Average clutch size of completed nests: 27.6 eggs.

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[1] Symbols in this column indicate the following:

F — freshly laid eggs; I — eggs had been incubated; S — short grass; T — tall grass; WI — eggs had been incubated for two weeks or more.

*Incomplete clutch.

one nest location and even after eggs were laid some males still moved away with the females.

Males at the New York Zoological Park built successful nests in both shaded and sunny areas. Raikow (1968) stated that in his study only nest sites in shaded areas succeeded. In Argentina, rheas often built in a shaded area or in tall grass (Wetmore, 1926). In my study, I found some nests in very sunny short-grass areas; however, of the more exposed nests, fewer succeeded as the weather got hotter near the end of the breeding season (Table 5).

Egg-laying

Raikow (1968), Sick (1964), and Steinbacher (1951) stated that males lead females to their nests for egg-laying. This could only occur for the first few eggs in each nest, since, from that point on, the male remained on the nest and females returned on their own each time they were ready to lay. Field observations in 1970 and 1972 indicate that males definitely lead females to their nests initially; but once the male remains on the nest the female must find it on her own.

Egg-laying almost always occurred just after midday in both wild and captive populations. Some females at the zoo laid within a 30-minute period every other day. In Argentina, I also observed that nearly all females laid with similar precision and at the same time of the day. I observed wild females lay a total of 23 eggs during October and November 1972, all between 11:00 and 15:00 hours.

Figure 13. A rhea nest showing the distinct ring of pulled vegetation around the nest.

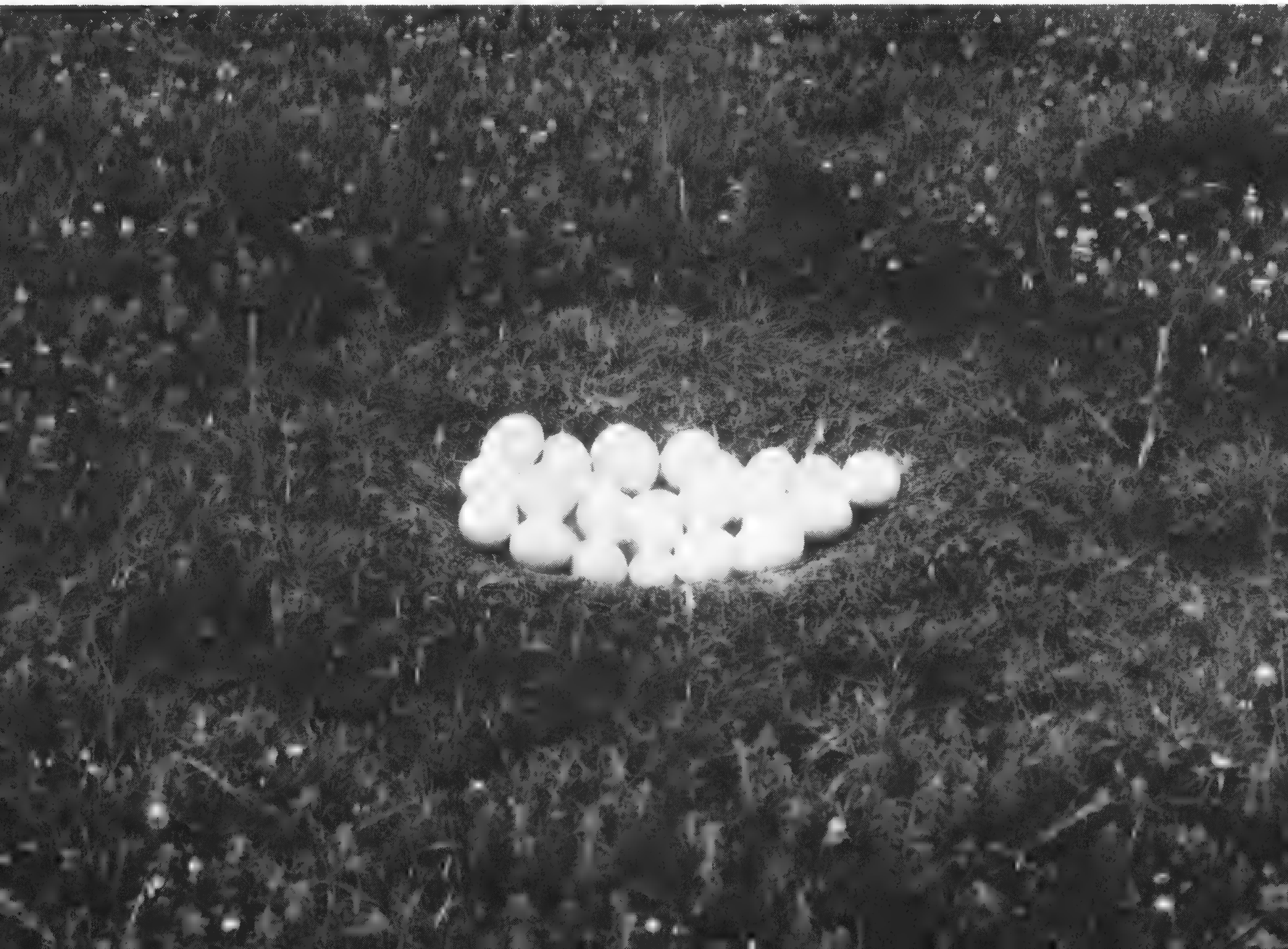

TABLE 5

Nests of Greater Rheas Observed in Argentina During 1972

Nest number	*Clutch size*	*Age of eggs*[1]	*Date first observed*	*Fate of nest*
1	20	F	22 October	Unknown
2	15	F	22 October	26 eggs abandoned 13 November
3	27	WI	22 October	54 eggs abandoned 13 November
4	3	F	22 October	Abandoned 24 October
5	16	I	22 October	Abandoned
6	3	F	22 October	Unknown
7	1	F	24 October	3 eggs abandoned 13 November
8	40	WI	23 October	Unknown
9	5	F	23 October	Abandoned
10	5	F	23 October	Abandoned
11	26	I	23 October	Abandoned
12	23	WI	23 October	Unknown
13	32	WI	23 October	Unknown
14	11	WI	23 October	Unknown
15	5	F	23 October	Abandoned
16	0	F	24 October	Unknown
17	8	F	24 October	Unknown
18	33	I	24 October	Abandoned
19	20	I	24 October	Unknown
20	10	WI	24 October	Unknown
21	10	I	24 October	Abandoned
22	15	WI	25 October	Unknown
23	1	F	25 October	Unknown
24	29	I	14 November	Abandoned
25	26	I	14 November	Abandoned
26	46	I	14 November	Abandoned
27	31	WI	14 November	Unknown
28	8	F	14 November	Unknown

Average clutch size: 18.1 eggs.

Average clutch size of completed nests: 26.1 eggs.

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[1] Symbols in this column indicate the following: F — freshly laid eggs; I — incubated; WI — well incubated.

The first egg or two may be laid in the nest or next to it; but after the first day, females deposit all eggs beside the male, who rolls them into the nest with his bill. The only exception occurred when a female approached the nest to lay after the male had left to feed or drink.

A nesting male became increasingly aggressive toward any rhea, including members of his harem, that approached his nest. Day by day females returning to lay their eggs approached more carefully. The male threatened each approaching female with a loud hissing sound and Head-Forward Threat Display. The female paused and acted submissively by flicking her wings, turning to the side, and lowering her head and neck. By assuming this submissive posture, and by failing to retreat in response to the male's threats, the female reduced his aggression, allowing her to move closer to the nest as the male quieted down. After several minutes, the male's aggressive behavior gradually became more ritualized, showing elements of the courtship display. The male's head swayed slightly, as it did during courtship. The neck-swaying coupled with the lack of threat display apparently acted as a releaser that allowed the female to continue her approach to the nest for egg-laying. The male frequently grasped the feathers of the female's neck and back with his bill when she approached closely. He continually kept the female in sight, often going through strange contortions while following every movement. It was not uncommon to see him with head upside-down looking directly over his back while continuing to hiss at the female as she slowly circled the nest (Figures 14–16).

As the female reached the nest abdominal contractions could be seen near the cloaca. The exact procedure for egg-laying varied greatly from female to female. Most females squatted on their tarsi. As the egg was pushed out by the cloacal sphincters, she either sat down fully or tilted her cloaca to the ground. Once the egg touched the ground, the female retracted the cloaca from around it and laying was complete (Figures 17-19).

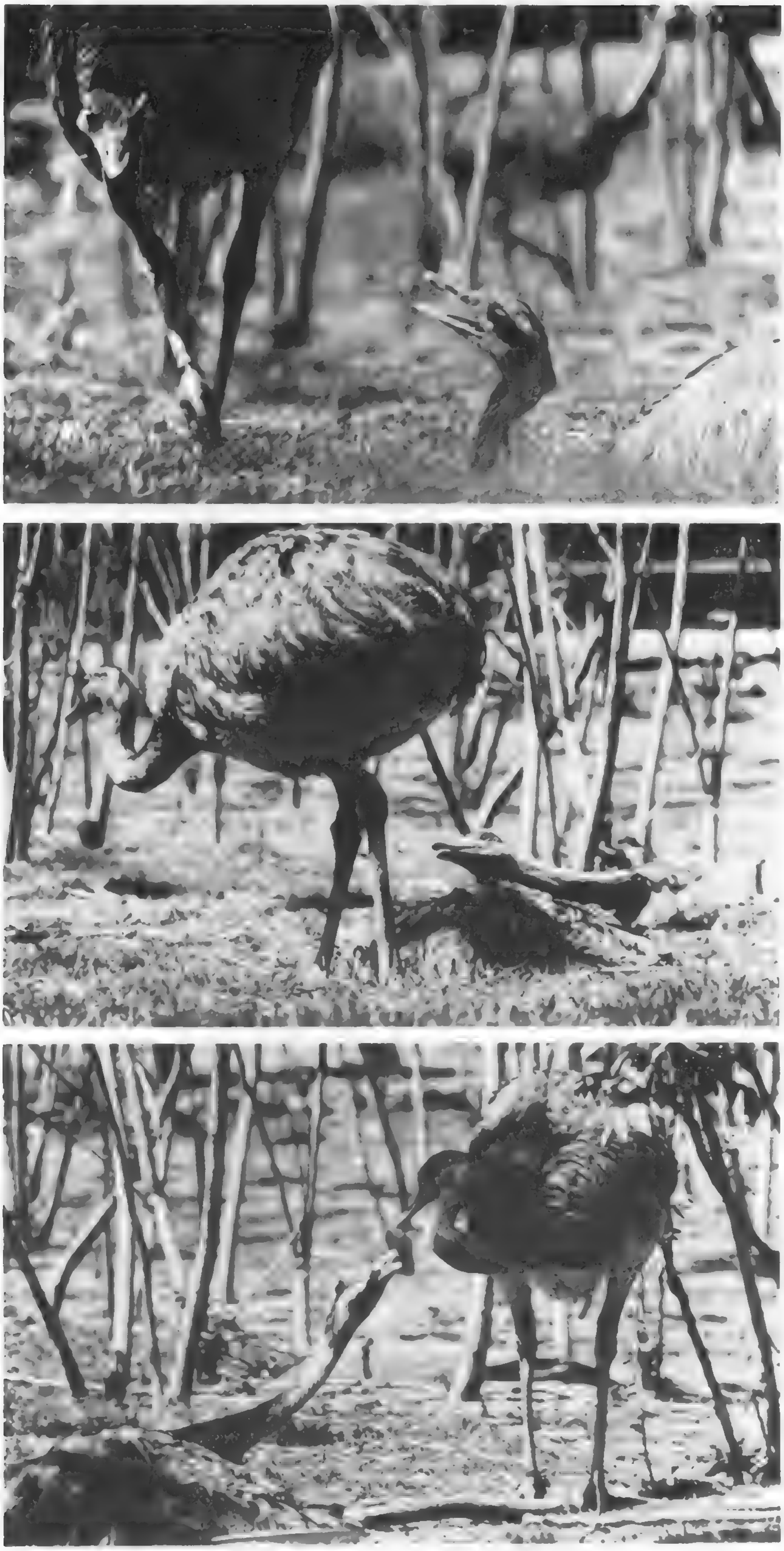
Portielje (1925) described an act in which the male extended one wing beneath the female's cloaca, catching the egg as it dropped so as to cushion its fall. I did not observe such behavior during the laying of over 30 eggs.

After laying an egg, the female stood up and walked away slowly, stopping to preen frequently. The male looked at the egg for a moment, and then reached out and rolled it into the nest with the underside of his bill. The entire egg-laying process took less than 10 minutes (Figure 20).

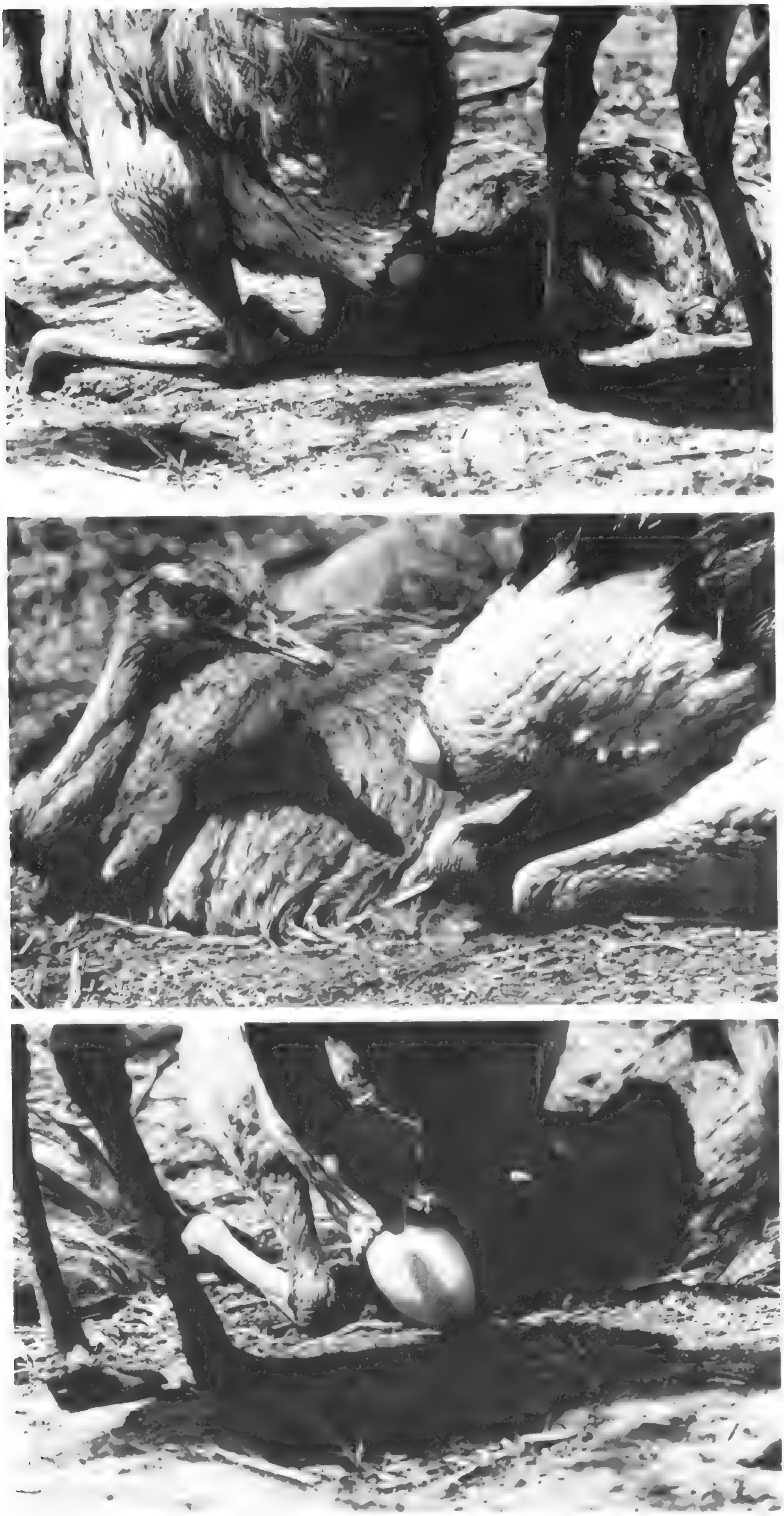
Egg-rolling

Since females lay their eggs outside the nest with few exceptions, the males have a strongly developed behavior pattern to roll them into the nest. In rheas, the male, under certain captive conditions, rolled eggs into the nest depression from 60 feet away. The maximum distance seemed to depend on its visibility from the nest site; an egg in heavy vegetation was less frequently rolled to the nest, even if it was within easy reach of an incubating male. Although I found many single eggs on the pampas, males there, or in captivity, failed to roll them unless easily visible from the nest.

As incubation proceeded, the male became more unwilling to leave the nest in order to roll eggs. By the end of the third week of incubation, he ignored eggs deposited more than five or six feet away. By the fourth and fifth weeks, he only rolled eggs within reach of the nest.



Figures 14–16. A male *(top)* hissing a threat to a female that approaches the nest to lay an egg. As she circles *(middle)*, he watches her continually. She assumes a submissive posture *(bottom)*, which gradually reduces his aggression.



Figures 17–19. A female *(top)* proceeds to lay an egg beside an incubating male and his nest, while the male *(middle)* watches intently; the female *(bottom)* deposits her egg on the ground.

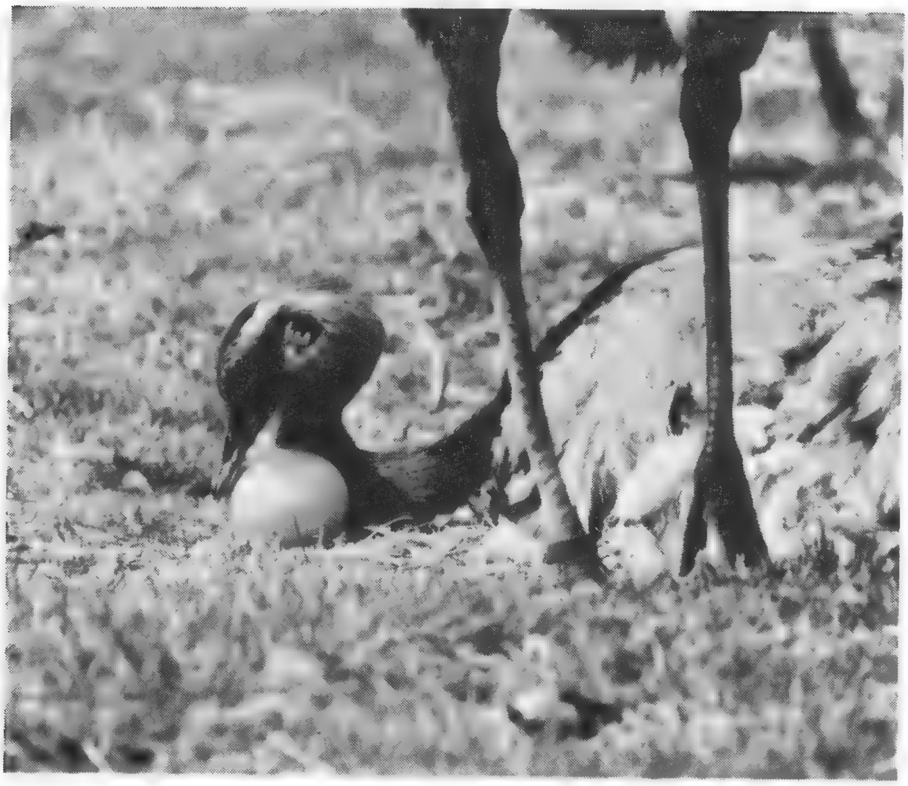


Figure 20. Male rolling a newly laid egg into the nest.

A young inexperienced male rhea responded to the first several eggs laid in a manner quite similar to what Lorenz (1938) describes as the normal egg-rolling act of the Greylag Goose. The young male first looked at the egg, then stretched out his head and neck toward the egg. Even if distracted, the rhea's gaze returned to the egg. The bill was slightly open as it explored the surface. The young male then extended the bill over the egg and rolled it back to the nest by pushing movements of the lower bill.

Once a male rhea had rolled a few eggs into his nest, the egg-rolling behavior became a more continual movement. The experienced male showed no hesitation and simply stretched out his neck to the egg and pulled it back into the nest.

At the New York Zoological Park, three different males were offered an assortment of eggs ranging in size from chicken and duck eggs to ostrich eggs. During the peak egg-rolling period, after three or four eggs had been pulled into the nest, a male rhea accepted eggs as small as swan eggs and as large as ostrich eggs if they were the proper color. Males investigated white to cream-colored eggs of chickens and ducks but did not roll them into the nest. Males stared at swan and ostrich eggs, touched them with open bill, and then rolled them into the nest. These results suggest that the elaborate procedure to investigate an egg before rolling it was an egg-recognition process during which the male determined the authenticity of the egg. This procedure prevented a relatively inexperienced male from selecting a rock, some other foreign object, or an alien egg to incubate. After one week of incubation, a male rhea seemed much more reluctant to accept either swan or ostrich eggs.

Color of Eggs

To further investigate the stimuli causing egg-rolling behavior, a number of plaster-filled rhea eggs were painted different colors and presented to three incubating males.

The results indicated the importance of color for male recognition of the eggs. The males only rolled yellow, light green to cream, or white eggs. They investigated other colors to greater or lesser extent but did not roll them into the nest.

Texture of Eggs

The texture of eggs also played a part in egg identification. Painted eggs of the right color were readily accepted. Texture only seemed to matter if the object was soft like a ballon or rubber ball; such objects the males investigated, pecked at, and frequently moved slightly, but never rolled them into the nest.

Shape of Eggs

Males accepted any rounded form. They rejected any object with a sharp edge, square corner, or irregularity. In final analysis, only rounded or egg-shaped objects without edges or corners were fully acceptable to a male rhea. Male rheas reacted to rough edges on an egg in the same manner as the Greylag Goose (Lorenz, 1938) — by pecking at all such edges and eating any pieces that break off.

Weight

Weight did not seem to be very important, as an empty rhea egg was rolled as readily as one filled with plaster. Inevitably, an empty egg was broken and the pieces of shell eaten.

Time of Year

During the non-breeding season or when courtship had just begun, I presented plaster-filled rhea eggs to displaying males on 10 occasions. A typical reaction occurred on November 13 and 27, 1971 when two plaster-filled rhea eggs were presented to a group of eight rheas. Three of the four males were displaying vigorously on both occasions. As soon as I placed the eggs on the ground, several males and females came to investigate. They immediately pecked at the eggs, but made no immediate attempt to roll them. After a few seconds of pecking and looking at the eggs, the male rheas once again resumed their displaying to the females. On several occasions, females, after pecking at the eggs, rolled them over once or twice before leaving. Within five minutes all rheas wandered off, leaving the eggs until they spotted them again a few minutes later and repeated the entire process.

It seems apparent that egg-rolling behavior occurs only after a nest-scrape has been constructed, suggesting that the male must be in an appropriate reproductive state before egg-rolling can take place.

Egg-rolling by Females

Females and very young males also rolled eggs on some occasions. This activity by captive females was mostly confined to rolling eggs into or out of a male's nest while he was away from the nest. Males usually left their nests to feed around midday, which was also the time of day that females rested nearby and laid eggs near the male's nest site. If a non-laying female happened to pass or see the eggs, she at least walked over to investigate the eggs and usually attempted to roll some of them. If a male was gone for an extended period, he returned to find his eggs scattered over a three-meter-square area. Females seldom rolled eggs more than a few meters; however, on at least two occasions at the Zoological Park, females rolled eggs five to seven meters from the male's nest. In both cases, the male probably could not see the eggs from the nest and he abandoned them. Egg-rolling by females on the Argentine pampas rarely occurred, since females wandered freely over large areas; captive females, restricted to the vicinity of the nest, rolled eggs quite frequently.

Incubation

Rheas began incubation two to three days after the first eggs were laid. This usually meant that between one-third and one-half of the clutch (10–50 eggs) was present in the nest before the commencement of incubation. By means of thermister probes inserted in rhea nests, I recorded the temperature of the eggs and the nest for six nests at the zoo and 14 in the wild. For the first two or three days, the male covered the eggs but apparently kept an insulating layer of feathers between his warm body and the eggs. As a result the eggs were only from one to ten degrees warmer than the soil on which they rested. The male started incubation by fluffing his feathers while settling on the nest, allowing his warm skin to touch the eggs. He then spread his wings over the nest on both sides. With each day, the male became more aggressive to the approach of any other rhea, and at the same time became more reluctant to leave to roll an egg back into the nest. By the second or third week of incubation, the male only rolled eggs within his reach and strongly threatened all rheas that approached the nest.

During incubation, males at the zoo left the nest for a short period during the warmest part of the day (Table 6), and ate continually until their return. The amount of time off the nest each day seemed to vary more with the air temperature and sunshine than it did with the stage of incubation (Table 6). On cool days, inattentive periods lasted only 10 or 15 minutes, while on a hot day males remained off the nest nearly an hour. The length of the inattentive periods seemed to increase slightly during the incubation period; however, this may simply be because the ambient temperature also rose during this period.

In Argentina, 22 incubating males left their nests between 11:00 and 16:00 hours; only two were observed leaving later. I observed the time off the nest for only six inattentive periods of six males, and they ranged from four to 32 minutes. Both the 32- and 21-minute periods occurred on relatively warm sunny days while the four-minute period occurred on a cool, windy day.

I observed 42 male rheas leaving their nest due to disturbances during this study. Each male reacted in his own way, depending on the type and proximity of the disturbance as well as on the stage of incubation that his nest was in. Sixteen males with incomplete clutches of 15 eggs or less all reacted to a disturbance by simply jumping up and running away from their nest with no special display.

Four other males with incomplete clutches jumped up when disturbed, but moved away performing some type of injury-feigning activity (Figures 21–23). One fluttered his wings slightly, two spread both wings and let them droop to the ground, and another dragged one wing on the ground while limping away from the nest.

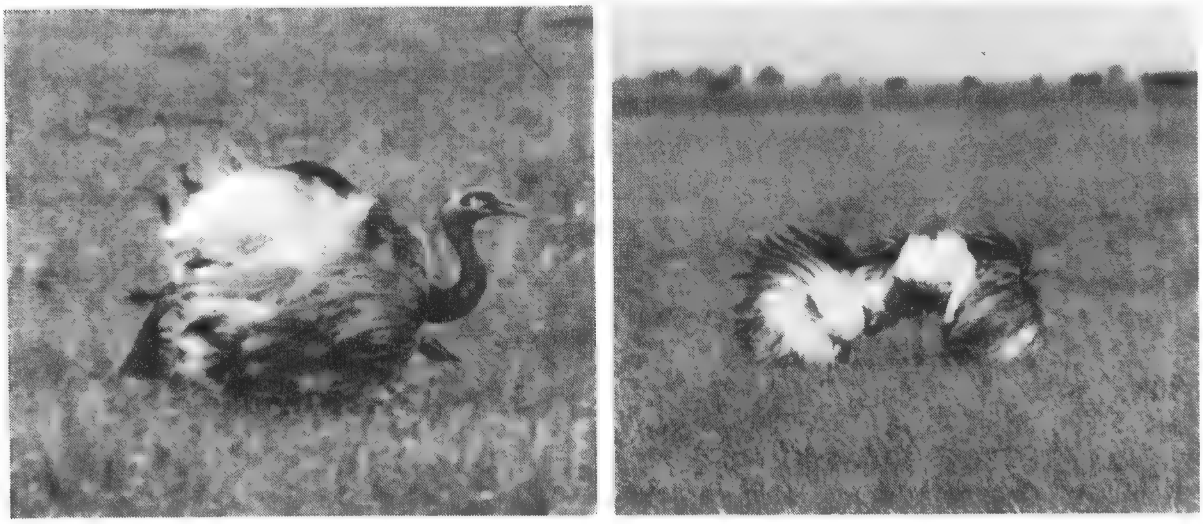
Nineteen males with clutches of 20 eggs or more performed broken wing acts when disturbed. These males ran from 10 to 50 feet from the nest before fluttering one or both wings and dragging them on the ground (Figure 21). Head and neck were generally drawn back against the body and held very low during this display. This activity occasionally continued for nearly five minutes but was usually restricted to less than three minutes or up to a distance of one-half km. The broken wing act slowly merged into preening and feeding behavior as the time and distance covered increased.

The last five males with complete clutches of eggs performed the broken wing act to some extent; however, these birds also feigned a broken, or injured, leg as well. Two of these males dropped onto their tarsi and shuffled along the ground appearing to be nearly helpless. The other three males developed a pronounced limp while dragging at least one wing on the ground.

In all these injury-feigning acts, the male exposed the white rump and underwing coverts (Figure 22).

While all males observed (n = 47) preened and fed as they moved slowly away from the nest after a bout of incubating, some males (19 of 47) made at least one quick dash from the nest when leaving to feed. They ran with an evasive zigzag pattern and with wings spread (Figure 23).

Males returning to their nests slowly moved closer while feeding. None of the rheas observed moved directly toward the nest once within approx-



Figures 21 and 22. A male rhea performs a "broken-wing" display to lead an intruder away from its nest.

imately 100 meters. Males carefully approached by feeding in a zigzag pattern while moving toward the nest. When within seven to ten meters, they became very alert with head and neck held high as they moved directly to the nest.

Once at the nest a male stepped very slowly and gently into the midst of the eggs. He vibrated the foot gently as he brought it down between the eggs. He placed the second foot between the eggs just as slowly and carefully as the first. As the male lowered himself onto the eggs, he swayed back and forth slightly so that the legs slid down between the eggs without breaking them. At the same time he spread the wings slightly and ruffled the feathers of the body so that the eggs made direct or nearly direct contact with the bare skin of the abdomen. After settling, the male rolled eggs around the periphery of the nest back under the body or wing. Each male observed, after positioning himself on the eggs then picked up a grass clump, twig, or bill full of dirt and tossed it over his shoulder. Some males repeated this procedure many times before relaxing completely on the nest.

In the wild a relatively small number of nests were successful (Tables 4 and 5). Rheas abandoned many nests when a rotten egg exploded or when disturbed too frequently by livestock or men. They deserted many nests for no apparent reason. Nests with more eggs than the male could cover were frequently abandoned when one or two rotten eggs exploded. This fact alone should play a strong role in selecting against a male that gathered too large a harem or retained the harem for too long a period.

Once the heat of summer arrived, most nests were abandoned. Disturbance by cattle, sheep horses, and most of all man probably contribute, but these do not seem to be the major factor. The semi-confinement by fences for cattle and sheep probably tend to allow higher than natural con-

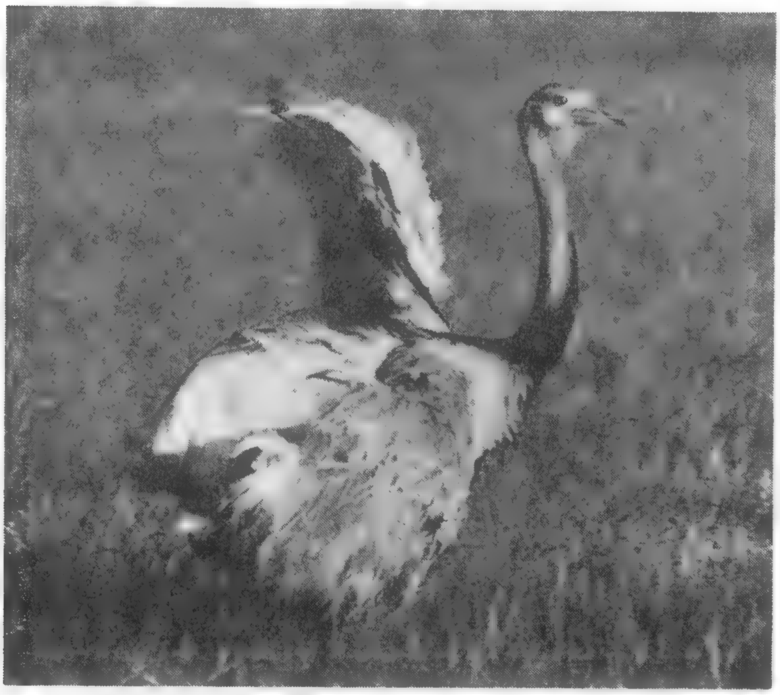


Figure 23. A male moving off at an oblique angle, using his evasive wing movements to attract attention.

TABLE 6

Times Incubating Male Rheas Were Observed off Their Nest in 1971

Stage of incubation	*Time off nest (in minutes)*	*Time of day nest was left*	*Temperature (centigrade)*	*Weather conditions*[1]
Day 2	3	13:00	18.9°	Cloudy, windy
3	5	12:10	22.2°	Cloudy, still
5	7	11:45	24.4°	Partly cloudy
7	12	14:00	24.4°	Sunny
9	6	13:30	20.6°	Clear
10	26	14:00	30.0°	Hot
12	2	13:15	20.6°	Cloudy, windy
15	10	14:00	21.7°	Cloudy
16	21	14:15	24.4°	Sunny
19	18	15:00	22.8°	Sunny
20	14	15:40	23.3°	Partly sunny
21	7	12:10	22.2°	Cloudy
22	9	13:00	23.3°	Sunny
24	39	15:00	27.2°	Hot
26	48	13:15	28.9°	Hot
30	18	13:00	24.4°	Sunny
31	11	13:30	22.8°	Clear
34	5	13:50	21.1°	Cloudy

[1] On six rainy days male did not leave his nest between 11:00 a.m. and 16:00 p.m.

centrations of rheas, which could contribute to the abandonment of nests. However, even the early surveys of Hudson (1920) and Wetmore (1926) indicated large numbers of stray eggs and abandoned nests.

At the Zoological Park, four young males developed nest-building and incubating behavior over a three-year period. At two years of age, all four young males built at least three nests, one even built a fourth, before settling at the final site to incubate. All four abandoned the nests and eggs within the first three weeks and only one of the four built another nest and tried again for 10 days before abandoning the second clutch.

During their second breeding season, three males once again built more than one nest. Two abandoned their nests after incubating 10 and 19 days, respectively. The third male managed to hatch chicks at his second nest site; however, he was very aggressive, killing one and injuring another before the remaining chicks were removed at two days of age.

During the third season, only two males were allowed to incubate, but all four constructed at least two nests each. One male, which hatched chicks the year before, successfully incubated a clutch and cared for five chicks. One of the other males became very aggressive after hatching his eggs; we separated his chicks.

TABLE 7

Comparison of Incubation Temperatures[1] in Wild and Captive Rheas

Nests of captive males						*Nests of males in Argentina*	
		Temperatures in nests					
Day of incubation[2]	*Ambient surface temp. .5 meter from the nest*	*Nest 1*	*Nest 2*	*Nest 3*	*Nest 4*	*Ambient surface temp. .4 meter from the nest*	*Temperatures in Nest A*
1	16.7	20.8	21.7		26.7	14.4	18.9
2	20.0	21.1	34.4	35.6	32.2	15.0	33.3
3	22.2	35.6	36.7		35.6	18.3	36.7
4	25.0	36.4	36.1			12.8	36.1
5	17.8	36.7	36.4	36.1	36.7	22.2	35.9
10	24.4	36.1	36.7	36.4	36.1	24.4	36.7
15	26.7	36.7	35.9	36.1	36.4	23.3	36.4
30	22.2	35.9	36.1			28.9	36.1
35	27.8	36.1					

[1] Centigrade.

[2] Starting from the time the first egg appeared in the nest.

Male rheas turn eggs at least once a week. Females turned eggs whenever they came upon an unattended nest with eggs.

Incubation Temperature

I determined the average incubation temperature of both captive and wild rheas by placing thermister probes into the nests among the eggs. Recordings were made after the male had been incubating for at least one hour. Nests of both wild and captive males averaged 36.4° C (Table 7). Experiments with artificially incubated eggs also indicated that a temperature between 36° C and 37° C produced the highest hatching percentage and the highest survival rate during the critical first week after hatching.

Freshly laid rhea eggs, being relatively large in size, retained heat for up to an hour after the brooding male left the nest each day. On five occasions when captive males left their nests to feed during the first 10 days of incubation, I recorded temperature changes of their eggs by means of a thermister probe taped to the bottom of an egg centrally located in the nest. Ambient air temperature on all five occasions was in the mid-twenties with no wind. All five eggs dropped three to four degrees centigrade within the first 30 to 40 minutes and fell within two degrees of the ambient temperature before a full hour had expired. During the incubation period, males seldom left the nest for more than 15 or 20 minutes around midday. Of a total of 64 absences (43 in captivity and 21 in Argentina) during the first two weeks of incubation, only five males remained off the nest for over 20 minutes, and on each of these five occasions ambient temperatures were in the thirties.

During the final five or six days of incubation, rhea embryos seemed capable of maintaining temperatures at, or above, 33° C. Temperature recordings on six occasions during this period showed that the egg temperatures did not drop below 33° C during the period when the male was off the nest. Sunshine prevailed, the air was still or moved with a slight breeze, and ambient temperatures were in the twenties on four occasions and in the low thirties on the other two occasions. Males were off the nest from 20 minutes to one hour and 10 minutes.

Of 126 inattentive periods (76 in captivity, 50 in Argentina) by incubating males, all except 17 occurred between 12:00 and 15:00 hours. One male left on a hot day at 10:15, five others between 11:00 and 11:59, and 11 walked off the nest between 15:00 and 17:00 hours.

The literature records an incubation period for the rhea ranging from 31 days (Butter, 1919) to 43 days (Fathergill, 1902; Heyst, 1950). My study indicates that on the average, eggs hatch after males incubate for 36 to 37 days, both in captivity and under natural conditions in Argentina (Table 8).

The great differences in reported incubation of rhea eggs were difficult to understand until some artificially incubated eggs indicated that mutual stimulation occurred within a clutch of eggs which induced synchronized hatching of the clutch (Table 8). Faust (1962) noted that rhea eggs laid as much as seven days apart can hatch within a 24-hour period. In the wild, synchronized hatching was very important, since the male left the nest 24 to 36 hours after the first chicks hatched. All eggs that had not hatched during this period were abandoned. This meant that eggs laid as much as eight to ten days apart had to synchronize their hatching if a maximum number were to survive.

TABLE 8

Incubation Periods of Rhea Eggs

	Average number of days
Artificially-incubated eggs	
10 solitary eggs	41
7 groups of 2 eggs each	38.2
34 eggs in groups of 3 to 6	36
43 eggs in groups of 6 or more	36
57 eggs in groups of 6 or more including 9 which were experimental eggs[1]	34.6
Experimental eggs hatched as follows:	
1 at 29 days, 1 at 30 days, 3 at 31 days, 4 at 32 days	31.1
Male-incubated eggs	
18 eggs hatched at New York Zoological Park	36.7
24 eggs hatched during study period in Argentina	36.6

[1] Experimental eggs were freshly laid eggs which were placed with groups of six or more eggs that had already been incubated for up to ten days to see if the fresh egg could be induced to develop and hatch with the older eggs.

Experimentally, I induced hatching as early as the 29th and 30th days of incubation by mutual stimulation (Table 9). I also prolonged incubation of a small percentage of the eggs from 41 to 43 days by isolating them from contact with other eggs. Hatchability was also greatly decreased in isolated eggs (Table 10). These experiments indicated the importance of mutual induction to synchronize hatching in the rhea.

Hatching

Rhea chicks pipped or began to break their shells from 10 minutes to 24 hours before hatching. The majority hatched within six to eight hours after the first break in the shell. The percentage of successful hatches decreased rapidly if the chick had not emerged within twelve hours after the first pip (Table 9).

Rhea chicks tended to pip between the midpoint and the large end of the egg, as do most birds (Nice, 1962).

In all cases the chicks ceased their muscular activity after the initial egg-shell fracture. This period varied from a few minutes to over an hour. Chicks vocalized frequently during this resting period and throughout the hatching process.

Due to mutual stimulation, artificially and naturally incubated eggs tended to hatch as a clutch over a six to eight hour period, even though they differed in age by as much as eight days. Rhea chicks frequently did not chip a circle around the egg during hatching as most other birds do. Instead, over 70 percent of the rheas observed enlarged the pip and pro-

TABLE 9

Hatching Success as Correlated to Time Elapsed Between Initial Pip and Successful Hatch

	Time between pipping and hatching			
	1–6 hours	*6–12 hours*	*12–18 hours*	*Over 18 hours*
Number of pips which died before hatching	4	7	15	10
Number of hatches	63	62	7	1
Total percent of hatches	95%	89%	32%	9%

duced additional cracks or holes in the shell before forcing the end out of the egg. The young rhea's powerful legs pushed against the larger portion of the shell, forcing the head and body out.

Post-hatching Behavior

Observations of over 50 newly hatched chicks indicate that the following account represents normal chick behavior during the first 24 to 36 hours. A newly hatched rhea chick stretched out flat for from 15 seconds to 15 minutes before further movements. The hatchling next attempted to struggle on its tarsus and sit up clumsily. These movements, interspersed with short rest periods, went on from five minutes to nearly an hour. Within one half hour after hatching the chick usually was sitting up. Frequently, much kicking and struggling accompanied the chick's attempt to sit up. Slowly, its ability to control the posture of the head increased; at first the head lay on its side on the ground, but as coordination improved the chick soon maintained its head in a normal upright position even when resting on the substrate.

At the same time, general body and leg posture improved as attempts to sit up became more coordinated.

TABLE 10

Hatching Success of Fertile Eggs: Groups Versus Solitary Eggs

Groups of Eggs		*Solitary Eggs*	
Number hatched	*Number in groups*	*Number hatched*	*Number incubated*
6	7	1	4
11	13	1	6
12	16	2	7
11	13	1	3
40	49	5	20
Hatchability = 82%		Hatchability = 25%	

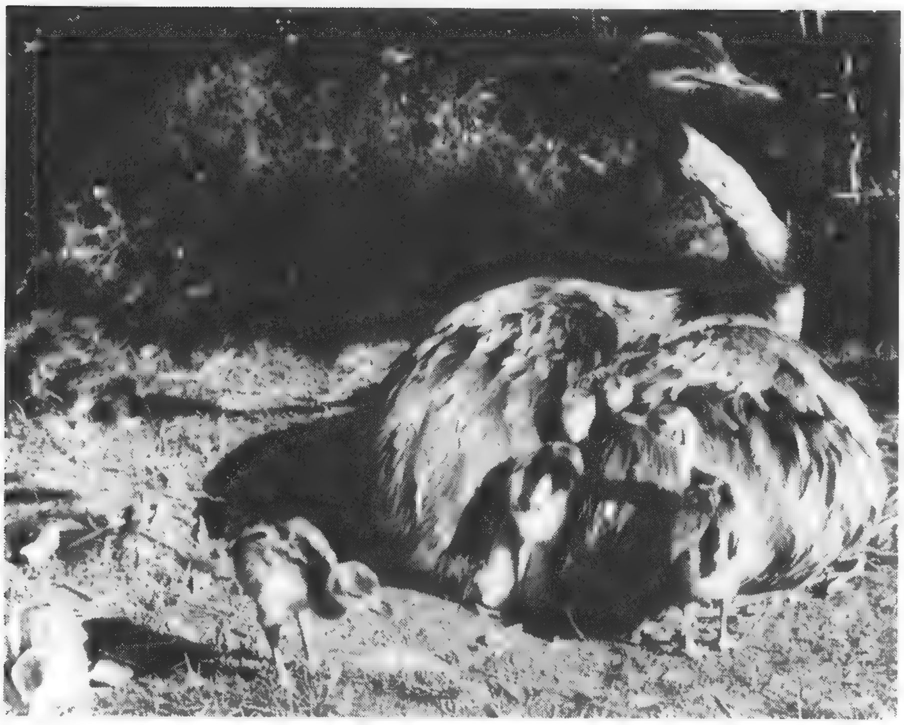


Figure 24. A male rhea with newly hatched chicks.

Even before the chick was able to maintain a seated posture, it attempted to stand up while struggling about on its tarsus. Within the first hour, nearly all chicks stood up and staggered a few steps before falling. In Argentina, I seldom heard the chicks call. Calling would be highly disadvantageous during this period.

For the next four to six hours the chicks spent some time sitting on their tarsi with head held erect. They were now capable of standing and running for short distances even if rather unsteadily (Figure 24). Chicks seldom maintained an erect position for more than five minutes, after which they rested for five to 30 minutes. About half of the rhea chicks started pecking at small objects and spots around them during this period. However, the chicks did not eat or even pick up food at this point in development. This early pecking for the most part was aimed at objects above the chick's head or at least above ground level. The above-head pecking of rhea chicks corresponds closely to the behavior described in Hazel Hen young by Kratzig (1939) and Pynnonen (1954). Nice (1962) called this behavior in galliform chicks "exploratory pecking."

Rhea chicks showed color and size preference for food particles much as do galliform chicks (Curtius, 1954; Hess, 1953, 1956a, 1956b). However, preferences for food items by rhea chicks changed with experience and time. Initially, green objects 2 and 5 mm in diameter were preferred, but soon shifted to larger sizes. Chicks relished moving objects like crickets, flies, and mealworms.

Behavior After Leaving the Nest

Chicks in the wild and in captivity remained at the nest and were brooded by the male for up to 36 hours. By this time, the chicks had emerged from under the male. As soon as the male stood up, the chicks clustered at his feet. The male then led the chicks off the nest, feeding continually as he went, but never losing his altertness to danger or threat. The chicks ran after the male and clustered at his feet whenever he stopped. The male rhea stood with neck outstretched, with head and chest both held high to be on the lookout for threats to the chicks. Males were extremely wary during the first few days and moved away from any possible danger unless pressed by an intruder, at which time they became very aggressive (Figures 25 and 26). As the male fed, the chicks followed his example. Since the male had not fed properly for several months, he did so almost continually for the first week, which stimulated the chicks to feed. Whenever a storm threatened or as dusk approached, the male trampled down an area of vegetation much the way he did initially for nest building. He often pulled clumps of grass and then settled down to brood as the chicks clambered under his wings.

Observations of 20 successful males in Argentina indicated that once the male left the nest with his chicks he did not return. Under the confining conditions of captivity, two males with chicks returned to the nest site each evening during the chick's first week. This difference in behavior probably represented a modification due to limited space.

The chicks followed the feeding male very closely for the first few days (Figure 27) and responded immediately to his call. Whenever the male became alert to some threat, his call brought the chicks into a cluster around his feet. If danger threatened, the male gave a signal and the chicks scattered in all directions, then hid by laying flat on the ground or under or beside a clump of grass; the male either chased the intruder away or distracted it with a broken wing display. After the male gave a soft bill-clapping sound, the chicks again clustered at his feet (Figure 26).

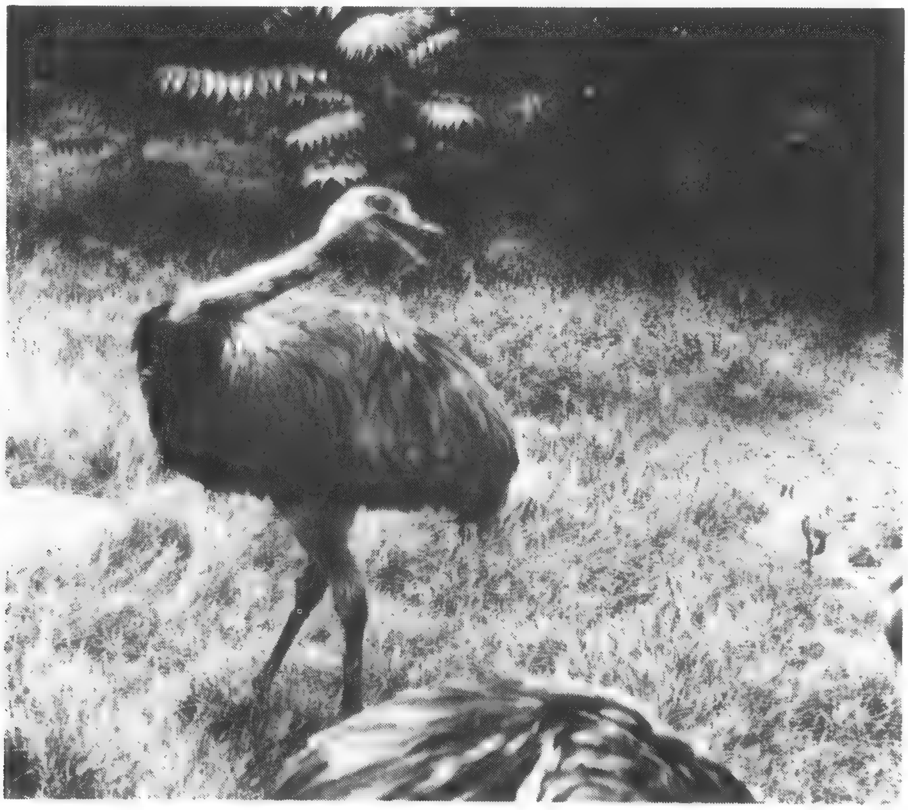


Figure 25. A female approaches too closely to a male with one chick, and receives the male's threatening display.

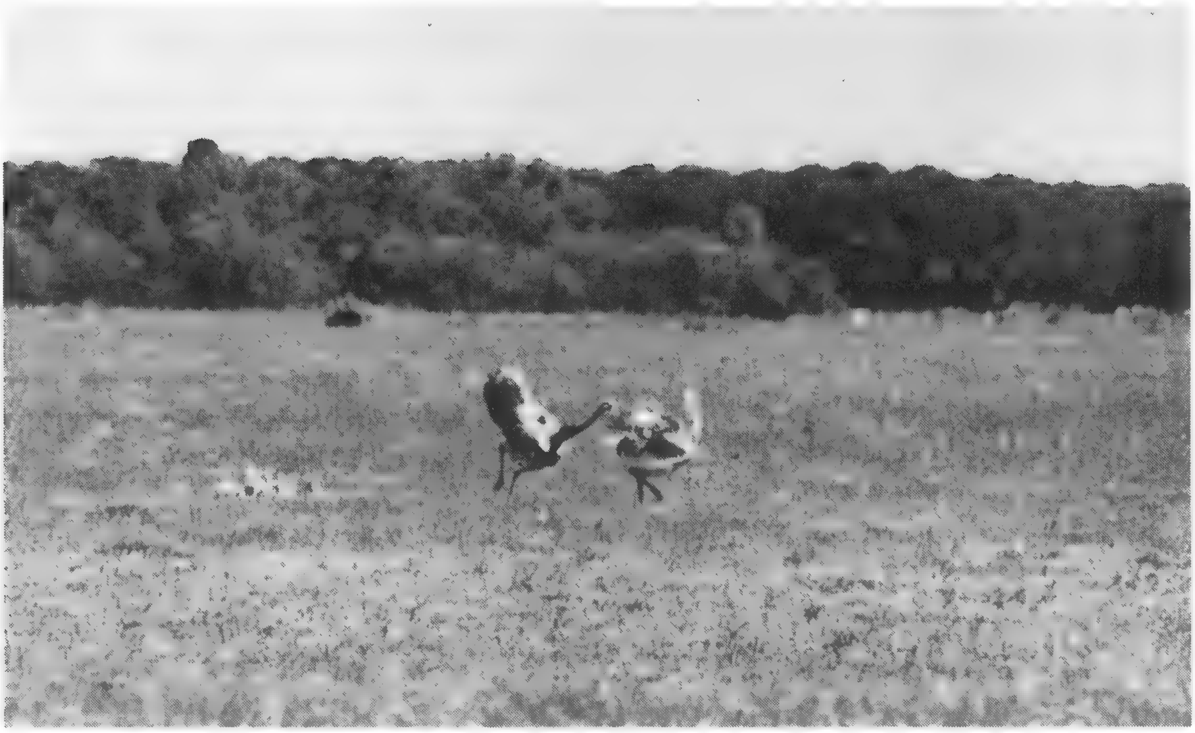


Figure 26. A male attacks a female as the chicks cluster behind the male.

During the first two or three weeks the male was extremely aggressive toward almost everything. Other rheas that wandered too close were savagely attacked.

Wild rheas in Argentina tolerated no other rheas within 18 meters of the chicks during the first week. At the end of one month, other rheas mingled with the chicks if they remained at least three to five feet from the male parent, and as long as no chick uttered calls to the male.

The chicks were in the most danger during the first few days after hatching. To survive, they had to keep up with their wandering father as he frequently covered up to five miles during one day. Crested Caracaras (*Polyborus plancus*) posed the biggest threat to young rheas, being almost always in attendance and waiting for an opportunity to take one as prey. The male rhea attacked any caracara that approached too closely either on the ground or from the air. In fact, he attacked any flying object larger than a butterfly — even private airplanes attempting to land in the vicinity of the chicks.

Possibly due to the rhea's special alertness toward aerial attack, caracaras more frequently attempted ground assaults. They could approach a group of chicks on the ground more closely than from the air before being attacked by the male rhea. A caracara was rather slow and awkward on a take-off from the ground, while a charging rhea was quite swift. As a result, the ground attacks were much more dangerous for the caracara. The male rhea struck mainly with his bill; but once an object was on the ground his feet became lethal weapons also. One rhea parent at the zoo killed squirrels, rats, and even pigeons.

Herds of cattle were another major threat to rhea chicks in their native Argentina. While cattle were accustomed to seeing adult rheas, they showed great curiosity about groups of chicks. In Argentina, a bellowing cow or bull running toward a chick often attracted others until an entire herd pursued a small chick. While the male rhea could attack one cow, he could not chase way a number of them. When the chick called and ran, it stimulated the cattle even more. Many chicks are probably trampled in this manner.

Disease and rain certainly caused major losses to chicks. Local Argentine landowners estimate that only five to ten percent survive (Barreto, pers. commun.). In captivity, heavy rains took a total of nearly 50 percent of the chicks less than a month old.

The chicks use an alarm call only when they are in immediate danger. The male responds to this call by charging toward the chick and viciously attacking anything in his way. The chicks also use a contact call to locate the male. The male responds immediately by moving in the direction of the call with the rest of the chicks.

The lonely plaintive call of a lost rhea chick was not uncommon on the pampas of Argentina during November and December. Since the males did not seem to identify their own chicks and the chicks seemed unable to identify their parent, lost chicks often ended up with another male. This lack of identity often resulted in one male ending up with a group of chicks ranging in age from newly hatched young to two months of age. If the difference was too great, the smaller chicks suffered due to a lack of brooding and protection by the male.

The chicks started feeding largely on vegetable matter, and clover seemed to be a favorite; but by the end of the first week the chicks chased insects vigorously. As they became alert to insects, the chicks held their heads high so that they could spot insects over much of the ground vegetation. The movements of the male actually served to stir up insects for the young as he walked through the grass in front of them.

At first the chicks ran after the male and picked at things around his feet only when he was feeding. Within a few days, they did not follow as closely. Day by day the chicks spread out farther while the male's alertness and aggressiveness gradually declined.

As the chicks grew, they fed on a larger proportion of plant materials. Eventually, as adults, they fed largely on broad leafed plants, some grass, a few insects, and even on plants like thistles, which are unpalatable for most other animals.

Captive chicks grew rapidly for the first three or four months, by which time they were nearly half of their adult size. When winter set in, growth was much slower. By the following spring, the young were still nearly one-third smaller than the adults. As a result, it is doubtful if rheas reproduce in the wild until they are two years old, although well-fed captive chicks have been known to reproduce when only one year old. In Argentina during the breeding season, I saw flocks of yearlings, which were slightly smaller than adults. Sometimes these flocks contained up to 40 young birds and a few non-breeding adults (Table 5).

Discussion

The Greater Rhea exhibits a unique social system. Avian mating systems are usually described in terms of the type, duration, and stability of the pair-bond (von Haartman, 1951; Van Tyne and Berger, 1959; Lack, 1968). Pair-bonds are usually considered either monogamous or polygamous (Van Tyne and Berger, 1959). Lack (1968) divides polygamy into three basic categories: (1) polygyny, in which one male maintains a pair-bond with more than one female, either simultaneously (harem polygyny) or in succession (successive polygyny); (2) polyandry, in which one female establishes a pair-bond with more than one male; and (3) promiscuity, in which no definite pair-bond is formed. The mating system of the Greater Rhea can best be described as harem polygyny and successive polyandry when compared to Lack's (1968) definitions. Astley (1907) was the first to suggest polyandry in rheas; but even today much of the current literature states that rheas are polygynous only (Lack, 1968; Welty, 1963).

The Greater Rhea exhibits a gregarious, but loosely cohesive, type of social structure during the non-breeding season.

Aggressive encounters during the non-breeding season, as well as during the breeding season, indicate that rheas have a male-dominated social structure. Contrary to the reports of Hudson (1920), Lack (1968), and Sick (*in* Thomson, 1964), rheas do not defend territories during courtship but simply defend a group of females. Only after a nest is constructed and eggs are laid does the male rhea actively defend the nest site, and even then it is only a small circle around the nest. The chicks, while vigorously defended when small, must fend for themselves within a few short weeks. Contrary to reports in the literature (Nice, 1962), rhea chicks are not fed by the male but gather their own food. The chicks depend upon the male for shelter, brooding, and protection, but feed entirely on their own. Chicks benefit from the male's movements, which stir up insects for them. The male serves an important function by feeding almost continually during the first week or two after chicks hatch, which stimulates the chicks' feeding behavior during this critical period.

Cooperative laying occurs to some extent in most ratites (Sick, *in* Thomson, 1964; Welty, 1963) and various tinamous (Lancaster, 1964a and 1964b; Schäfer, 1954). Although Lack (1968) states that two to four hens lay in one rhea nest, the current study indicates that in both wild and captive birds up to 15 females lay for one male before moving on to lay for another male. This cooperative breeding system of rheas can then be best described as polygamous with successive polyandry.

Lack (1968) speculates that natural selection could favor a cooperative breeding system if the following three conditions were met: (1) a reversal of sex roles; (2) the necessity for only one parent to raise the young; and (3) a surplus of females. The first two conditions definitely occur in rheas; but the third condition, if it occurs, raises many more questions than it answers. An unequal sex ratio can develop in nature in several ways. Since there seems to be no differential mortality in chicks, any imbalance from equity must occur in adult, or nearly adult, birds. Single males and nesting males could certainly be more susceptible to predation. However, field observations during the current study indicated very little, if any, natural predation on adults. Historically, in the recent past, there have been few predators capable of killing adult rheas. Due to man's hunting activities over the last hundred years, young males driven away from protected areas could certainly be killed in greater numbers than the less mobile females. However, even if this occurs today, it probably was not as significant a factor several hundred or several thousand years ago. Without detailed studies of past and present predators, this problem cannot be resolved.

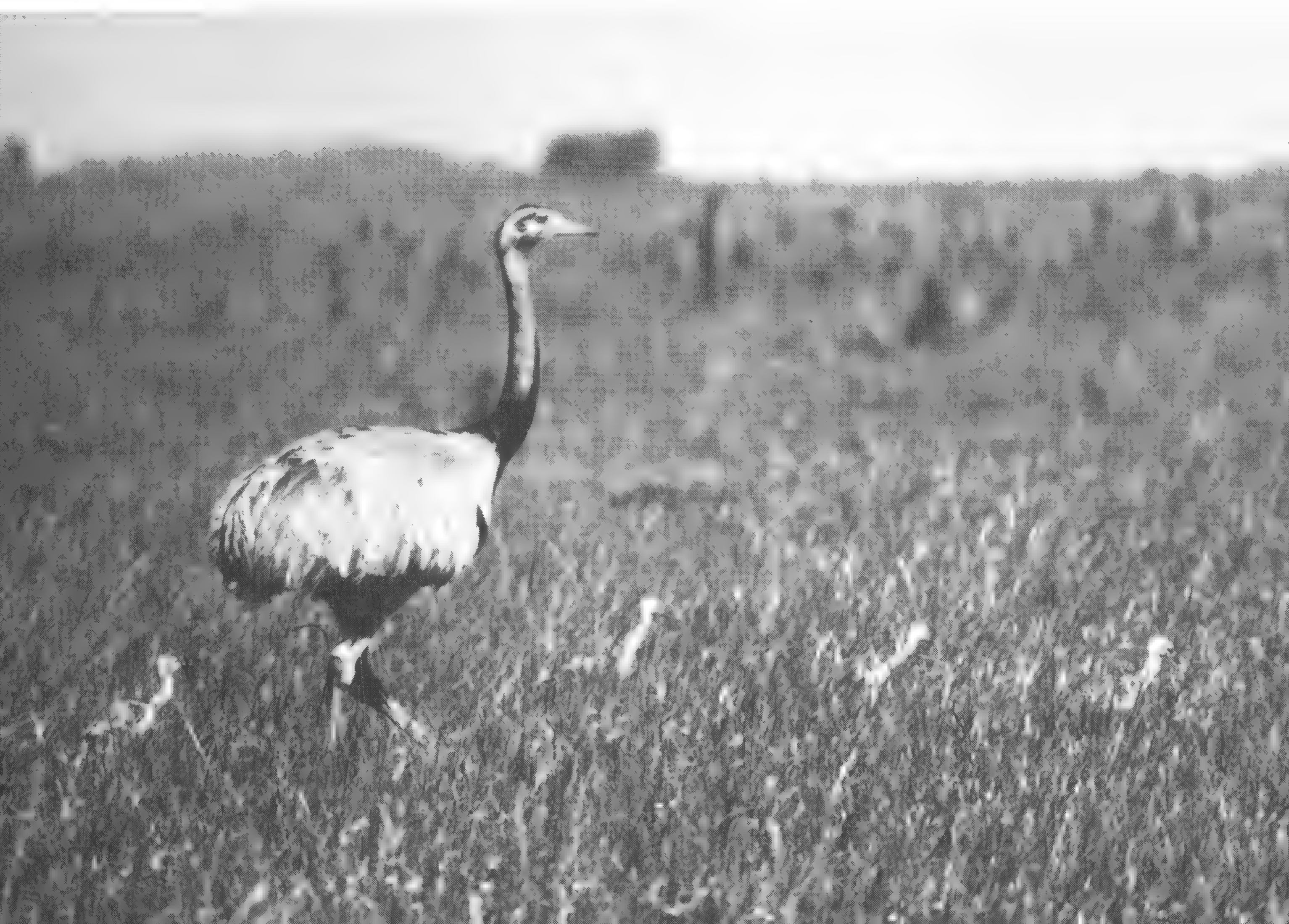
The current study does not indicate an unequal sex distribution of adults. Inadequate methods of sex determination of adults and the fact that so many males were nesting made accurate total counts difficult; but the small difference between numbers of males and females counted on a single day suggested that no significant difference existed in the study area in Argentina in 1970 and 1972.

Selection has probably favored this system because it permits the production and incubation of a maximum number of eggs. The adult rhea's omnivorous, but largely vegetarian, diet on the vast pampas of Argentina apparently does not restrict or in any way select against the production of vast numbers of eggs. Rheas seemed to have little competition for the vast assortment of plant material until the introduction of domestic cattle and sheep.

The large numbers of abandoned nests seem very ill-adaptive; however, if most nests were successful, the pampas would be covered with rheas. The large number of abandoned nests may simply be due to man's elimination of natural predators and his land-use practices that have confined flocks of rheas in abnormally high concentrations. However, even the early reports of Hudson (1920) and Wetmore (1926) indicate that large numbers of abandoned nests and stray eggs occurred before intensive ranching had begun. Large numbers of rheas do not survive their first winter; and essentially all rheas abandon their nests with the onset of hot summer weather (Barreto, pers. commun.). These facts probably help explain why such prolific egg production evolved.

Rheas have developed the highly adaptive behavior of synchronous hatching, first described and studied in quail by Vince (1964a, 1964b, 1966a,

Figure 27. Week-old chicks following the male parent.



1966b, 1968a, 1968b). Faust (1960) was the first to suggest that rheas might synchronize their hatching. Since induction in rheas can occur several days before the normal incubation period is over, synchronous hatching must involve methods other than those described for quail by Driver (1967), Gottlieb (1968), and Vince (1969), all of which depend on sounds produced by chicks after the bill breaks into the air cell. The fact that rheas can hatch a full week before normal incubation is over strongly indicates that movements or sounds produced by chicks long before breaking into the air cell must have some stimulatory effect.

Even though the reproductive system of the rhea is uniquely distinct from that of most birds it shows a close resemblance to the systems of other ratites and tinamous. Lancaster (1964a and 1964b) described breeding systems of tinamous in which several females contribute to a clutch incubated by a single male. In Ostriches, several females likewise contribute eggs to one nest (Austin and Singer, 1961; Crandall, 1929). The male incubates at night and helps care for the young; however, the dominant female incubates during the day and cares for the chicks (Sauer, 1959; Van Tyne and Berger, 1959). Cassowaries are not thought to be polygamous, but the male incubates the eggs (Austin and Singer, 1961; Lack, 1968). The male emu also incubates the eggs of one or two females (Lack, 1968).

The similarities in the reproductive behavior of ratites revolve around the male incubating the eggs. Only in the ostrich does the female share the responsibility of incubation and care of the young. These duties are left solely to the male tinamou, rhea, cassowary, and emu.

Several females contribute to one male's clutch of eggs in all except the cassowary. However, there are no reports of more than three, or rarely, four female tinamous, ostriches, or emus laying in one nest. My study indicates that up to ten or twelve female rheas contribute to one male's clutch of eggs.

Summary

The Greater Rhea (*Rhea americana*) exhibits a gregarious but loosely cohesive type of social structure during the non-breeding winter season. A weak male-dominated social hierarchy exists within the gregarious wintering flock, but is not prominent. Except between the most dominant males, individual distances are maintained with little aggression.

With the onset of the spring breeding season, the social structure changes significantly. A strong male hierarchy emerges as the flocks break up into smaller units consisting of one or two competing males and a harem of up to fifteen females. Male rheas establish their dominance by driving off other males and defending a group of females.

Male rheas do not maintain a territory during courtship. Once a nest site is established, a small area is defended by the male. The size of this "territory" is only slightly larger than the individual distance normally maintained by a male rhea. Generally, a simple threat consisting of lowered head, gaping bill, and a low hissing sound is enough to maintain this spacing between them. Even when two dominant males oppose each other, it is unlikely to go beyond threats or an occasional chase. Only during the breeding season do fights erupt. Fights between males are ritualized pushing matches in which the combatants grasp each others' bills while trying to throw each other off balance.

Once the male has demonstrated his dominant position, he must attract the seemingly uninterested females with his wing-spreading and head-swaying displays. Following the group of females, the male's display intensifies; and the females slowly start to respond. Over a period of two or three days, a definite shift occurs as the females begin to follow the displaying male.

When the females start following the male, he is ready to mate and to construct his nest. For a full week, the females return to the nest-site to lay their eggs. Since the male is on the nest most of the time, females lay their eggs near the nest-depression rather than within it. The male subsequently rolls the eggs into his nest. Incubation and rearing of the young are left to the male. This now occupies the male's time, while the females move off with another displaying male.

The eggs hatch synchronously. The male leads the chicks to food and stimulates their feeding by his own feeding behavior, and carefully protects and broods them.

The most conspicuous aspect of rhea reproductive behavior is the dominant role played by the male. He performs courtship displays, builds the nest, incubates the eggs, and rears the young, while the female's role is limited to mating and egg laying. The rhea is both polygamous and polyandrous with no lasting pair-bonds formed.

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PATTERNS IN THE LIFE HISTORIES OF STORM PETRELS ON THE FARALLON ISLANDS

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Storm petrels (family Hydrobatidae) are among the least known families of marine birds. They are among the most pelagic of avian species, and they usually breed on comparatively distant and inaccessible islands, where they not only spend relatively little time but usually are active only at night. They nest out of sight in deep cavities or burrows, and desert their nests readily when disturbed. At sea, where storm petrels spend most of their time, their small size (Figure 1) and erratic flight render them inconspicuous and difficult to observe at length. Finally, because of subtle differences in size and color between species and subspecies, much confusion exists over their taxonomy, especially in those forms nesting on islands off the California and Baja California coast (Austin, 1952; Crossin, 1974). Often times, an observer at sea in this area is not sure which form he is seeing, even after he collects it and makes comparisons with known specimens.

Two hydrobatids, the Leach's and the Ashy Storm Petrel (*Oceanodroma leucorhoa* and *O. homochroa*), nest on South Farallon Island, California, with respective breeding populations numbering 1,600 and 4,000 individuals (Ainley and Lewis, *in press*). So similar are they in morphology and in what was previously known about them that we decided to take a closer, more careful look at their life patterns. These two species on the Farallones are identical in the general shape of their bodies, tails, wings, feet, and bills. They also are nearly identical in size, although statistically distinct differences can be seen with large enough samples. Standard measurements taken by Loomis (1918) reveal the following differences for central California birds: *leucorhoa* averages eight millimeters larger in wing chord and1.4 mm larger in culmen length; but *homochroa* averages five mm larger in tail length and 0.4 mm larger in tarsus length. On the average, the Leach's outweighs the Ashy by no more than three grams. It has been known for some time that both species nest at about the same time of year (Bent, 1922), and that their nest sites are interspersed on the same rocky talus slope of the eight-hectare southern quarter of the island. A study of *homochroa* conducted by James-Veitch (1970) revealed the Ashy to be almost indistinguishable in nesting habits from the several other storm petrels so far studied (see Allan, 1962; Beck and Brown, 1972; Gross, 1935; Harris, 1969; Scott, 1970). The most pronounced difference previously noted between the two species is in color: the Ashy being entirely dark, and the

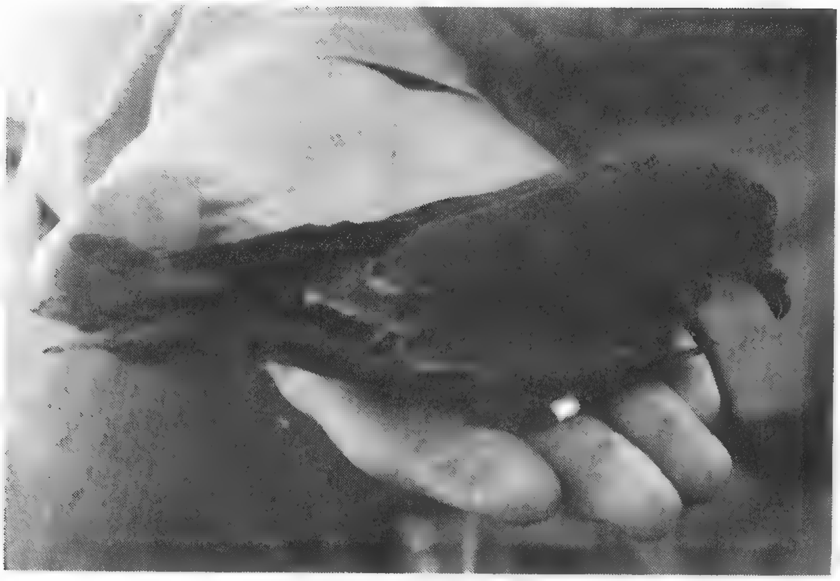


Figure 1. An adult Ashy Storm Petrel rests in the senior author's hand. Photograph by Ian C. Tait.

Leach's equally dark except for a flashy white rump patch. Thus, before us was a natural problem for study: how do these little known but very similar species differ biologically in ways that allow them to nest together on the same island.

Methods

South Farallon, a rocky granitic island 44 hectares in area, and its neighboring islets rise at the edge of the continental shelf at 37.4°N, 123°W, 43 kilometers due west of San Francisco's Golden Gate (Figure 2). Oceanographically, the Farallones lie within the California Current. This rich cold-water current flows south along the coast of Oregon and California, displacing warmer subtropical waters westward, before turning west to become part of the North Equatorial Current of the tropical central Pacific. Twelve species of marine birds, totaling 250,000 breeding individuals, nest on South Farallon (Ainley and Lewis, *in press*).

The major effort in this study was expended from April 1972 until April 1973, although included in this report are data collected in adjacent years. At least two of us were present on the island throughout the period. We divided the calendar year into 73 five-day periods and attempted to capture 30 individuals of each species during every period. We report here on data taken from 981 Ashy and 321 Leach's Storm Petrels. We captured the birds at night by playing tape recorded calls of *leucorhoa* to attract both species to mist nets placed on the talus slope. After each capture session, we banded the birds, recorded data, and released them one by one while it was still dark. One of us measured and banded while the other recorded. We weighed each bird to the nearest 0.1 grams on an electric balance, measured its wing, and recorded its molt. We characterized the incubation patch on a scale of 0 to 5: downy, partially downy, bare, vascularized, refeathering, and refeathered but with evidence of scaly skin.

Wing loading was determined for 32 birds of each species during the last week of May 1973 (Period 29). After weighing the birds, the outstretched right wing of each was traced on paper. The figure obtained by measuring this tracing with a planimeter, to determine enclosed area, was multiplied by two to give the total wing area. This figure divided by the body weight gave the loading in grams per square centimeter of wing surface.

We recorded egg-laying dates in 1972 and 1973 for the Ashy Storm Petrel ($n = 62$) and in six years, 1968 to 1973, for the Leach's Storm Petrel ($n = 8$). The fewer egg dates for *leucorhoa* was due to the greater inaccessibility of their nests. In the case of four Leach's, we knew only the hatching or fledging dates, and determined the egg-laying date from knowledge of incubation and fledging periods (Table 1).

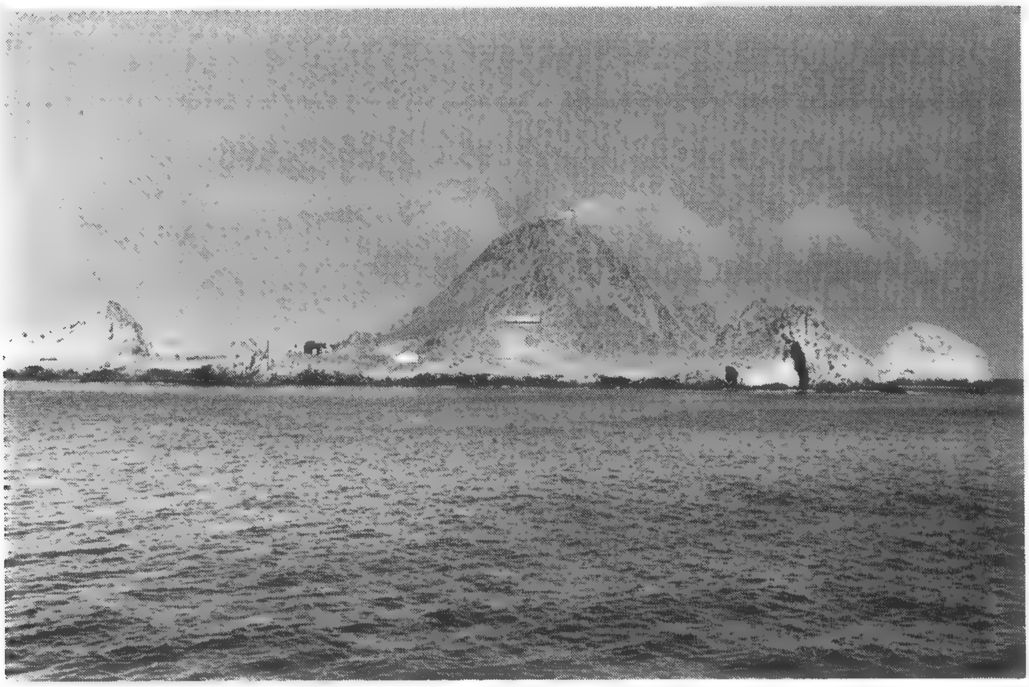


Figure 2. South Farallon Island is a small, rugged, and rocky island located off San Francisco in the cold California Current. The storm petrels nest on the southern end of the island on the flat area to the left of the buildings and on the rocky slopes above them. Photograph by Ian C. Tait.

Morphological Comparisons

We already mentioned the close similarity between these two storm petrels in general color (except rump), shape of body parts, and size. However, interesting differences in two aspects of their morphology are important to factors discussed later in the paper.

First, a comparison of body weight with the pre-egg and nesting periods revealed that both species weighed their maximum during the pre-egg stage when they were finishing, or had just finished, molt (Figure 3). In these early weeks of island visitation, Leach's averaged 41.9 gm, 2.3 gm heavier than the average Ashy at 39.6 gm. By the end of the nesting season (Period 40–46), when chicks were almost fully grown, Leach's had dropped to 38.7 gm, only 0.6 gm heavier than the average Ashy (38.1 gm). Thus, both species gradually lost weight but *leucorhoa* did so at a much faster rate. Statistical comparison of the regression lines for weight change (Figure 4) indicated that the two species lost weight at different rates. After Period 46, the apparent weight increase in Ashys probably reflected weights of birds carrying food to their chicks. Upon capture, this species did not regurgitate its stomach content as readily as did Leach's. Thus, toward the end of their respective nesting seasons, we more likely weighed Ashys with full stomachs and Leach's with empty ones; therefore, we did not include Ashys in the regression analysis after Period 46. The general trend, in which maximum weight is attained prior to egg-laying and is then lost during incubation and chick-rearing, has been described in some other petrels (Fisher, 1967; Richdale, 1947; Scott, 1970). Later, we discuss the interesting difference in the rate of weight lost by the two storm petrels.

The second morphological comparison, that of wing loading, revealed that *leucorhoa* carried less weight per unit wing area than *homochroa*. This probably allows Leach's less energy expenditure per unit distance traveled. The average wing areas for *leucorhoa* and *homochroa* were, respectively, 236.6 cm² and 193.4 cm²; and the average wing loadings in late May were, respectively, 0.16 gm/cm² (SD = 0.011, n = 32) and 0.20 gm/cm² (SD = 0.012, n = 32). The difference in wing loading, although small, was highly significant statistically ($P < 0.001$). Over the nesting season, however, wing loadings are unlikely to remain the same because of seasonal change in body weight, and with due consideration to the possible effects on wing areas by feather wear and molt. Our observations show that most feather wear is restricted to fraying of the outer two to three mm of the longest primaries in some individuals. This probably does not affect wing area significantly, and we regard the wing areas as effectively unchanged by feather wear. On the other hand, Ashys molt the first two primaries when still feeding chicks, which results in a loss of effective wing area of about 5 cm² or about three percent. This loss is almost fully compensated by seasonal weight loss, and thus wing loading remains little changed. Wing loading, then, decreased in Leach's Storm Petrel from 0.18 gm/cm² during the pre-egg period to 0.16 gm/cm² by the late chick-period; but for Ashy Storm Petrels, wing loading remained at about 0.20 gm/cm² (an actual change of 0.003 gm/cm² occurred) for the entire nesting cycle.

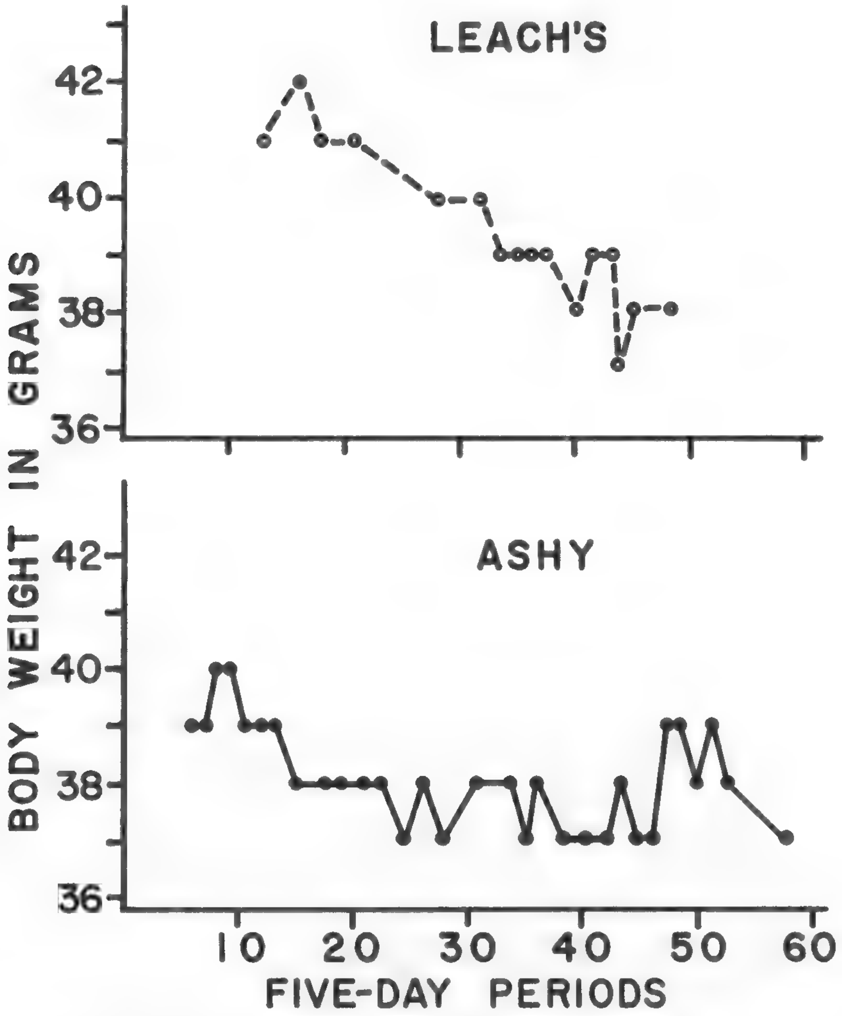


Figure 3. The change in body weight of the two storm petrels during the pre-nesting and nesting period. Points represent mean weights for birds captured during five-day periods. After Period 20, we did not include weights from birds with downy incubation patches (immatures).

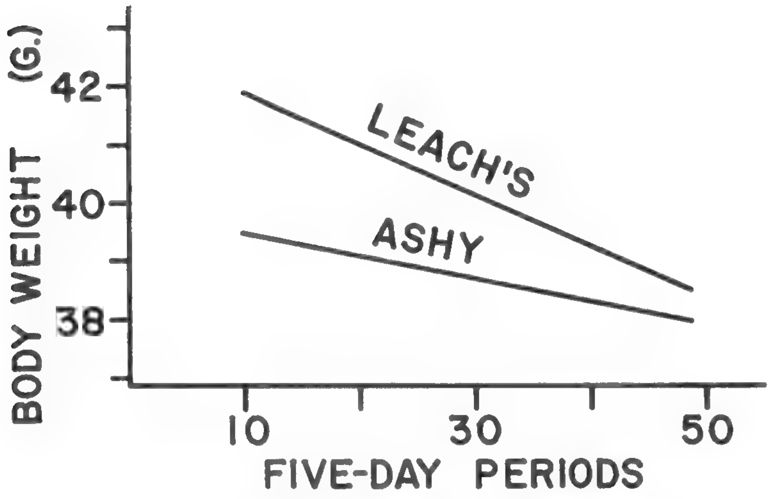


Figure 4. Regression lines for weight changes in the two storm petrels. Points used to calculate the lines are the mean value in Figure 3 between Periods 11 and 49, the time span during which Leach's Storm Petrels are present on the island. The difference between the slopes (for Leach's, $r = -0.927$; for Ashy, $r = -0.811$) is statistically significant ($P < 0.001$).

Oceanic Distributions

The Leach's Storm Petrel in the North Pacific is a bird of the open ocean and rarely occurs close to the coast (Figure 5). During the period from 1955 to 1973, accounts in *Audubon Field Notes* and *American Birds* reported less than 25 Leach's Storm Petrels within 80 km of the California coast between Point Conception and Cape Mendocino (40.5°N), a north-south distance of about 800 km (summarized in Ainley, MS). The Pacific Ocean Biological Survey Program (Crossin, 1974; King, 1970) reported this species as one of the most abundant birds of the ocean area between Hawaii and North America from September to May, and uncommon, but present,

TABLE 1

Comparison of Nesting in Two Storm Petrels

	Ashy	*Leach's*
Egg Size (percent body weight)	21.6[1]	20.16[2]
Incubation period (days)	44	42[2]
Days to fledging	76	66[2]
Total nesting time (days)	120	108
Adult weight loss	6.3%	10.3%

[1] Data from James-Veitch (1970).

[2] Data from Gross (1935), Huntington (*in* Palmer, 1962).

during other months. On a fall trip from Hawaii to central California, Alan Baldridge (pers. commun.) noted *leucorhoa* a few times each day until he reached 300 km from the mainland coast; thereafter, he saw none.

The Ashy Storm Petrel has a very different oceanic distribution (Figure 5). It is confined to waters just seaward from the edge of the continental shelf and essentially to the waters of the California Current off California and northern Baja California. Where the edge of the shelf lies within 15 km of the beach in Monterey Bay (80 km south of the Farallones), up to 7,000 Ashys are seen each summer and fall. At other times of the year, they occur there in fewer numbers, and many times up to 20 birds have been observed a few kilometers west of the Farallones. We know of no reports of this species in mid-ocean.

Comparison of their oceanic distributions thus indicates that, first, *leucorhoa* ranges widely in the open ocean and *homochroa* remains closer to the island and to the coast. Second, Leach's prefers the warm subtropical waters westward of the California Current while the Ashy prefers the cold waters of the current. The lesser wing loading of *leucorhoa* is compatible with its greater mobility.

Our work on food preferences has just begun, but data collected thus far support the different oceanic distributions of the two species. The stomachs of four Leach's and eight Ashy Storm Petrels all contained small fish eye lenses and cephalopod beaks; however, the stomach of one Leach's contained individuals of the siphonophore, *Vellella vellella,* an invertebrate characteristic of the open ocean (Hubbs, 1948). All this agrees with the observations of Martin and Myres (1969), who reported that *leucorhoa* is associated with warm oceanic water and *Vellella* westward of the coastal current off British Columbia.

Patterns of Attendance at the Colony

Annual Cycle

Leach's Storm Petrels visited the island for about twenty-seven weeks (195 days) beginning the last week of February and ending the first week of September (Figure 6). The adult population reached its peak about mid-March. Included were breeding birds and probably physiologically mature non-breeders as well, based on studies of other storm petrels (Beck and Brown, 1972; Harris, 1969; Scott, 1970). When chicks began to fledge the first week of August, the number of adults visiting the colony declined sharply.

During the first three weeks of June, large numbers of immature Leach's visited the island (forming the large peak in Figure 6), and could be readily distinguished from adults by their completely downy incubation patches and their browner plumage (because of its greater age). Late season visits by immatures have been described for albatrosses (Fisher and Fisher, 1969; Richdale, 1950), shearwaters (Harris, 1966; Richdale, 1963), and storm petrels (Scott, 1970); but in other tube-noses, immatures visit early in the breeding season (Beck and Brown, 1972; Harris, 1969).

Our mist-net captures showed that Ashy Storm Petrels came ashore over a much more extended period of island visitation, at least 325 days. We captured some birds in every month except for a period of several weeks in late November and early December (Figure 6). However, some adults must have visited at that time, since we banded recently fledged chicks in December and January. Thoresen (1961) also found adults feeding young in January. Following the first visits of the new cycle in late December, the adult population increased to its peak by the beginning of February and then remained at that level for several months. The first chicks began to fledge in late August and the majority fledged by mid-November. Throughout the fledging period, the number of visiting adults slowly declined.

Immature Ashys, also recognized by their downy incubation patches and their lighter plumage color, began to visit in early April, much earlier than immature Leach's. They continued to visit until early July, although the low recapture rate of banded immatures suggests that few of them made repeated visits during this period. In June 1972, we captured two one-year-olds banded as chicks the previous year. Thus, even immature *homochroa*

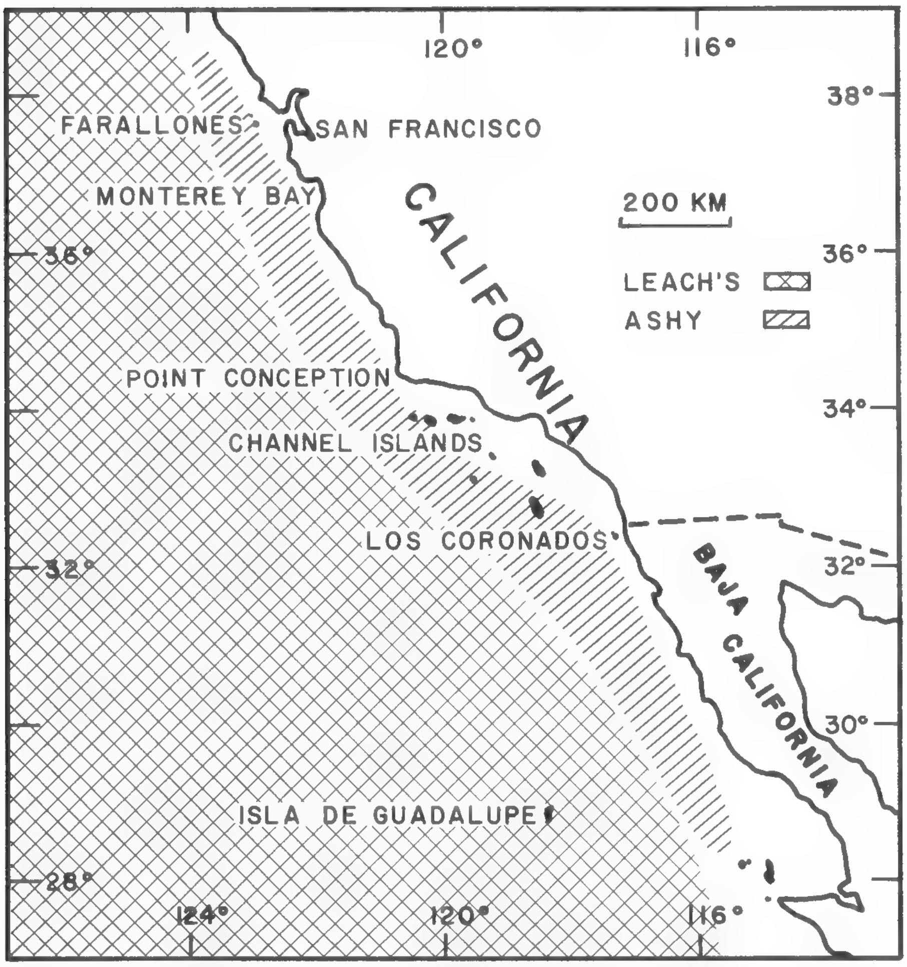


Figure 5. A generalized sketch of the oceanic distributions of Leach's and Ashy Storm Petrels off California and Baja California drawn from the following information sources: *Audubon Field Notes* and *American Birds* (1955 to 1973); AOU Check-list, 1957, A. Baldridge (unpublished observations at sea); Crossin, 1974; King, 1970; and Martin and Myres, 1969. The eastern boundary of the Leach's range was set according to the observations of A. Baldridge and also the approximate western edge of the coldest part of the California Current and the usual eastern edge of oceanic water. The Ashy and the Leach's Storm Petrels, respectively, seem to be associated with these two distinctly different oceanographic areas. We do not argue the fact that there is probably overlap of the ranges — to what degree is yet unknown — or the fact that at certain times or places Leach's Storm Petrels may occur closer to the coast during daylight. Much remains to be learned about distributions of marine birds in this area.

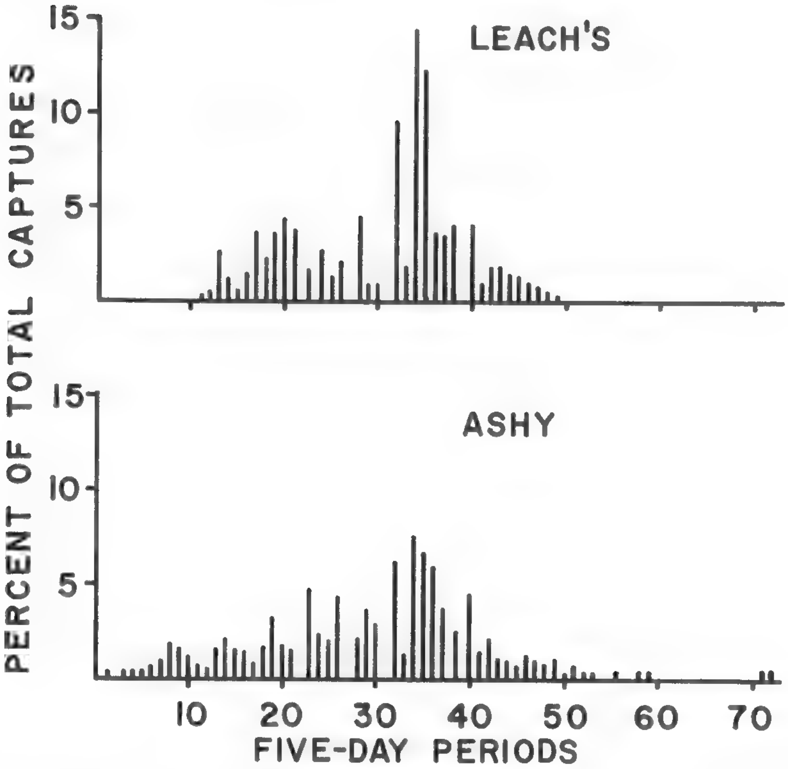


Figure 6. The annual pattern of island visitation for the two species as drawn from capture data. The peaks between Periods 30 and 40 for Leach's Storm Petrels and between 19 and 40 for Ashy Storm Petrels indicate visits by large numbers of immatures. Other data indicate that some Ashys are present between Periods 60 and 70.

visited over a more extended period than their *leucorhoa* counterparts, something like 100 days versus 20 days, respectively. Also, immature Ashys began to visit prior to egg-laying, whereas Leach's immatures began visits during late egg-laying in their respective cycle. Beck and Brown (1972) and Harris (1969) hypothesized that early season visits by immatures of storm petrels they studied were an anti-predator strategy. For Leach's and Ashy Storm Petrels, apparently subjected to the same predator pressure on the Farallones, the markedly different patterns exhibited by the immatures suggest that predation is not the determining factor. Rather, we suspect that visitation routines of the immatures are determined by the same factors affecting corresponding differences in visitation routines of the adults.

Nightly Pattern of Island Visitation

Differences between the two species include their patterns of nightly visitation (Figure 7). Both species arrived, flew about, visited their burrows, and departed the island only during the night. Ashy Storm Petrels arrived in large numbers as soon as complete darkness occurred. Most birds captured then, and for the next hour or so, had just arrived as suggested by their full stomachs. After this initial peak, the number of birds arriving or flying about declined to a lower level that continued throughout the remaining hours of darkness. During the middle hours of the night, we captured mostly immatures with downy incubation patches. The adults must have been in their nests at that time. With the coming of twilight at about 04:00, all birds either departed or entered nests for the day.

Leach's, in contrast, did not really begin to arrive in large numbers until an hour after darkness fell, at about 22:00 hours; and their peak ar-

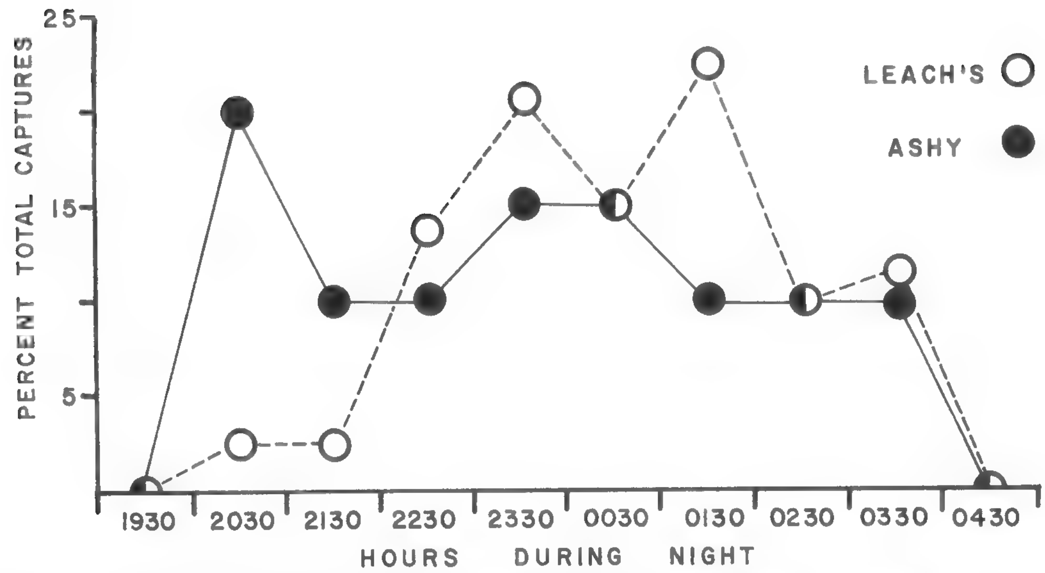


Figure 7. The nightly pattern of island visitation as drawn from capture data during 10 nights between Periods 19 and 35. The times shown are the beginnings of successive hour-long periods (Pacific Daylight Time). Darkness occurs at about 21:00 hours.

rival did not occur until midnight. Captures continued high for about two hours, then declined. As with their annual patterns of visitation, *leucorhoa* also spent more time away from the island each night than did *homochroa*. The Leach's Storm Petrels probably needed those initial hours of darkness for the flight from their more distant feeding areas.

Patterns in Egg-laying

We used two methods to determine the patterns of egg-laying in the two species. The first was the traditional method of plotting egg-laying dates; and the second, because of the small sample of known laying dates for Leach's Storm Petrel, was a comparison of changes in the incubation patch during the year.

Egg-laying by *leucorhoa* on the Farallones, based on eggs of known or calculated laying dates, extended from the second week of May until mid-June (extreme from 9 May to 16 June; Figure 8), a period of 38 days or five-and-one-half weeks. Most of the eggs (75 percent) were laid during the three-week period from 19 May to 6 June. Egg-laying dates in *homochroa*, on the other hand, extended from late April into mid-July (extremes from 30 April to 17 July), a period of 79 days, twice as long as in Leach's. Most eggs (75 percent) were laid by Ashys during the six-week period from 19 May to 1 July; however, they have laid eggs as late as early September, as indicated by the 10 fledglings we have banded since 1970 during December and January. Thoresen (1960), too, observed adults feeding young in January. The Ashy thus has an extended asynchronous egg-laying, as observed by Orr (1946) and James-Veitch (1970), compared to the rather synchronous egg-laying of the Leach's.

We confirmed the patterns described above with information on incubation patch changes. Passerines, and many other avian groups, lose the down on their incubation patch within a few days of egg-laying. With the onset of incubation, the skin of the patch becomes heavily vascularized. The close timing of these changes provides criteria for determining when eggs are laid. This, however, is not so in storm petrels (Harris, 1969; pers. observ.) and penguins (Ainley, 1974), in which breeding birds, and even physiologically mature and immature non-breeders, lose the down from their patches up to a month or more before egg-laying. Furthermore, in the Ashy, at least, we found it difficult to determine whether the skin of the incubation patch was vascularized even in a bird removed from its nest while incubating. We could, however, correlate certain characteristics of the incubation patch to hatching. Between two and ten days after hatching, down feathers begin to grow on the incubation patch, which in three to four weeks, becomes completely refeathered with down (n = 15). We assume the pattern to be similar in Leach's. By correlation of re-feathering to egg-hatching and by extrapolation, we can describe the egg-laying of the two species.

The first re-feathering patch found in *leucorhoa* (Figure 9) appeared on 21 June (Period 35) and the last was found on 29 August (Period 49). In some individuals, the patch should have begun to re-feather within two days of hatching, so the first egg probably hatched on 19 June. If we count back 42 days from this date, which is the incubation period in this species (Table 1), we arrive at 19 May as the probable egg-laying date — the same date, by coincidence, of our first egg-record for Leach's. If we next count back 38 days (the maximum time needed for re-feathering of a patch after egg-laying) from the date of the last re-feathering patch, we arrive at 23 July as the latest hatching date. Extrapolating from this, 11 June becomes the latest egg-laying date, four days earlier than our observation of an actual egg laid in a nest (Figure 8). Thus, the incubation patch data confirm the pattern of egg-laying drawn from our meager number of Leach's egg dates. Similarly, the incubation patch data for the Ashy also agree with the pattern drawn from their egg-laying dates (Figure 10).

Both methods of analysis thus indicate an extended asynchronous laying period in *homochroa* compared to the contracted synchronous laying in *leucorhoa*. Egg-laying completely overlapped in the two species, since both began to lay at about the same date. This contradicts the hypothesis that two sympatric species of storm petrels do not have overlapping periods of egg-laying (Cody, 1973). We will say more below about the factors that affect the timing of egg-laying in these two species on the Farallon Islands.

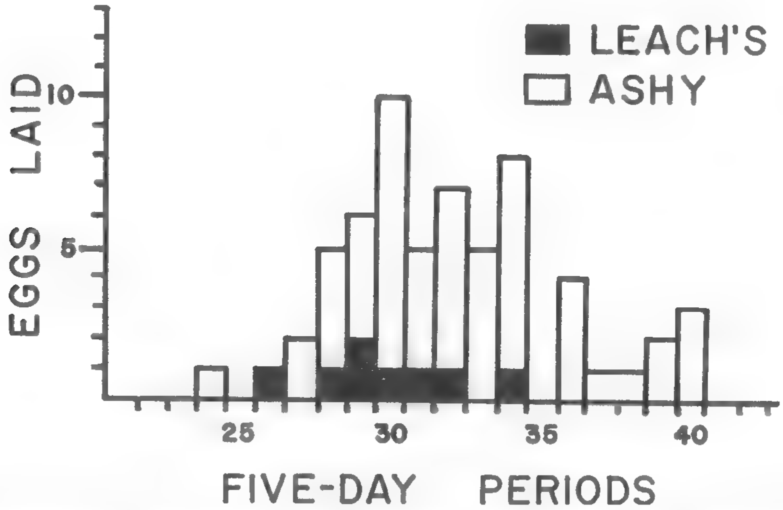


Figure 8. The egg-laying periods of the two storm petrels at the Farallones. Represented are the dates of egg-laying by eight Leach's and 62 Ashy Storm Petrels.

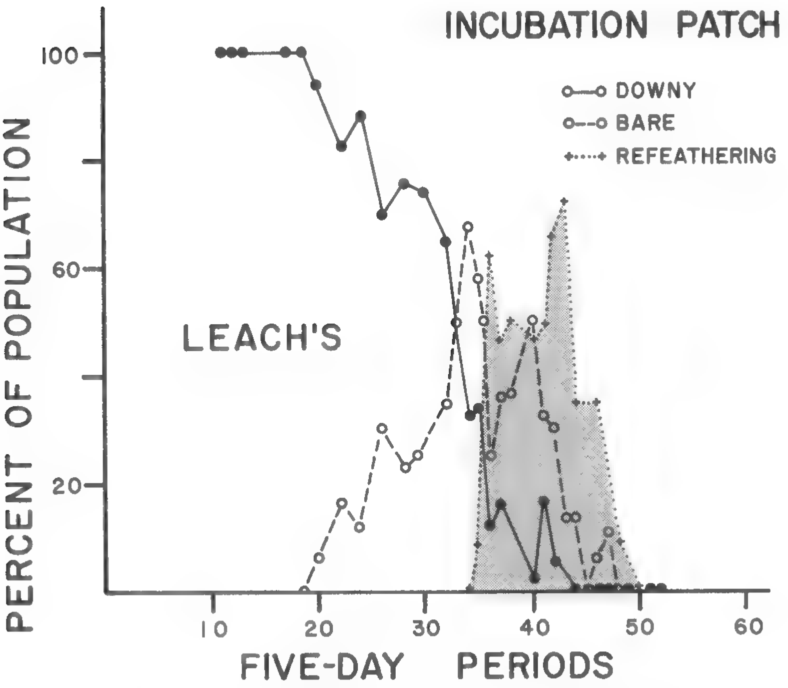


Figure 9. Changes in the stage of development of the incubation patch for the population of Leach's Storm Petrels over the course of the pre-nesting and nesting seasons. The shaded area highlights re-feathering patches which indicate the stage of nesting.

Pattern of Molt

The sequence of molt and a comparison of its intensity and timing in these two species will appear in detail elsewhere (Ainley *et al.,* MS). At this point, we wish to discuss the degree of overlap between molt and breeding. In breeding birds of both species, molt of body feathers began around the time of egg-hatching in mid-June (Figure 11). A few weeks later, the parents' tails began to molt, and after a few more weeks molt in the wing began. In

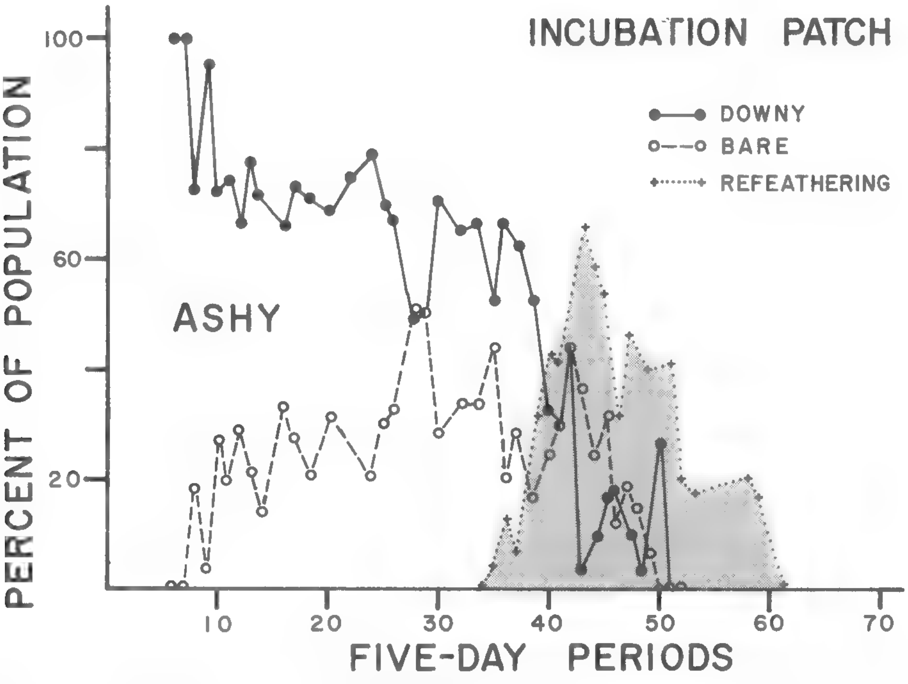


Figure 10. Changes in the stage of development of the incubation patch for the population of Ashy Storm Petrels over the course of the pre-nesting and nesting seasons.

leucorhoa tail molt began much sooner relative to other phases in the molt, and was completed more rapidly than in *homochroa*. Since Leach's chicks grow more rapidly, most young fledged earlier in the molt cycle of their parents. This meant that Leach's parents, for the most part, departed from the island for their winter quarters after they completed their tail molt but had not begun the wing molt. In contrast, all breeding Ashys were well into tail and wing molt by the time their chicks fledged.

When Ashys began to visit the island during the pre-egg stage of the following breeding cycle, they still were molting their flight feathers. A few months later, at the end of March, they had finished. In contrast, wing molt of Leach's Storm Petrel overlapped very little with the pre-egg stage of their nesting cycle, because their first visits to the island were delayed until mid-March. Both species required about the same amount of time for molt, and both started and finished at about the same time of year. The difference lay mostly in the more contracted occupation of the island and nesting cycle of *leucorhoa,* which allowed that species to undergo most of its molt during the wintering period. The different degrees of molt and breeding overlap in these two storm petrels are largely similar to patterns compared in other long-ranging versus short-ranging procellariiform groups (see Warham, 1967; Scott, 1970).

Some Characteristics of Nesting

The final comparison involves certain aspects of nesting (Table 1). The Ashy lays a slightly larger egg that takes two extra days to hatch. In addition, the Ashy chick requires, on the average, 10 more days to grow to maturity. Chicks of both species fledge at about adult weight (unpublished data). Overall, there is a difference of almost two weeks in the time required by the two species to produce a chick. This difference provides a basis on which to speculate about the different rates of weight loss during the course of the pre-egg and nesting periods. Simply stated, *leucorhoa* may have to work harder to raise its chicks than *homochroa.* Since they feed much farther from the island than the Ashys, Leach's Storm Petrels must log many more miles of daily travel during the shorter time in which they raise their young. Little wonder, then, that Leach's adults lose proportionately more weight from the higher energetic requirements to which they are subjected during the breeding season than do Ashys. Even the slight advantage *leucorhoa* has in wing loading does not equalize their efforts. It seems very likely that in order to breed on the Farallon Islands, Leach's Storm Petrels are over-extending themselves a little, at least compared with Ashy Storm Petrels there. Perhaps *leucorhoa* nesting on the Farallones fly farther to suitable feeding areas than populations of this species elsewhere. However, if they are to breed at all off central California, these islands offer the only suitable site. The species' nearest nesting areas to the Farallones are 384 km to the north and 450 km to the south (AOU, 1957). Why the Leach's Storm Petrel avoids feeding closer to the islands and to the coast is a question that needs further investigation.

Discussion

Thus far, comparison of several patterns in the life histories of the two storm petrels indicates that differences in their routines of island visitation and nesting habits seem to be determined largely by differences in their habits away from the island. An investigation of storm petrels on Ascension Island and a consideration of nesting studies in other hydrobatids led Allan (1962) to postulate that the really important differences between storm petrels should be in their behavior and ecology away from breeding colonies. Our discoveries in this study agree with this prediction.

To be sure, Farallon storm petrels do share major similarities in the patterns of breeding: both nest in the same habitat of the same island, and both lay their eggs at the same time of year. Complete overlap in egg-laying is probably related to predation by Western Gulls (*Larus occidentalis*). Each year of the past three (1970–1972), we found, without much effort, the remains of 50 or more storm petrels in gull pellets. Also appearing in the pellets were 15 of 2,326 bands placed on petrels in 1971 and 1972. Thus, almost one percent of the storm petrel population, or about 50 birds out of 6,600 fall prey to Western Gulls at the breeding grounds each year. Cavity-nesting and nocturnal activity in storm petrels have already been

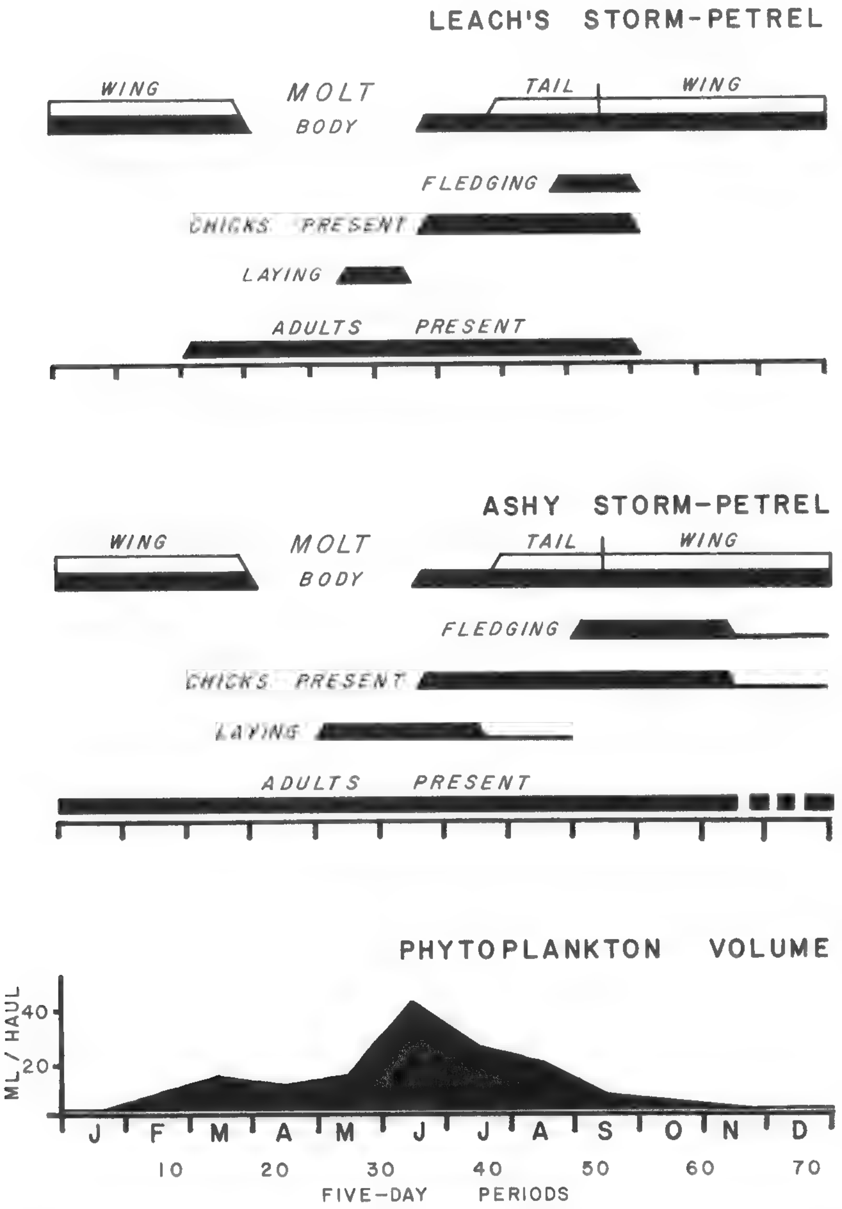
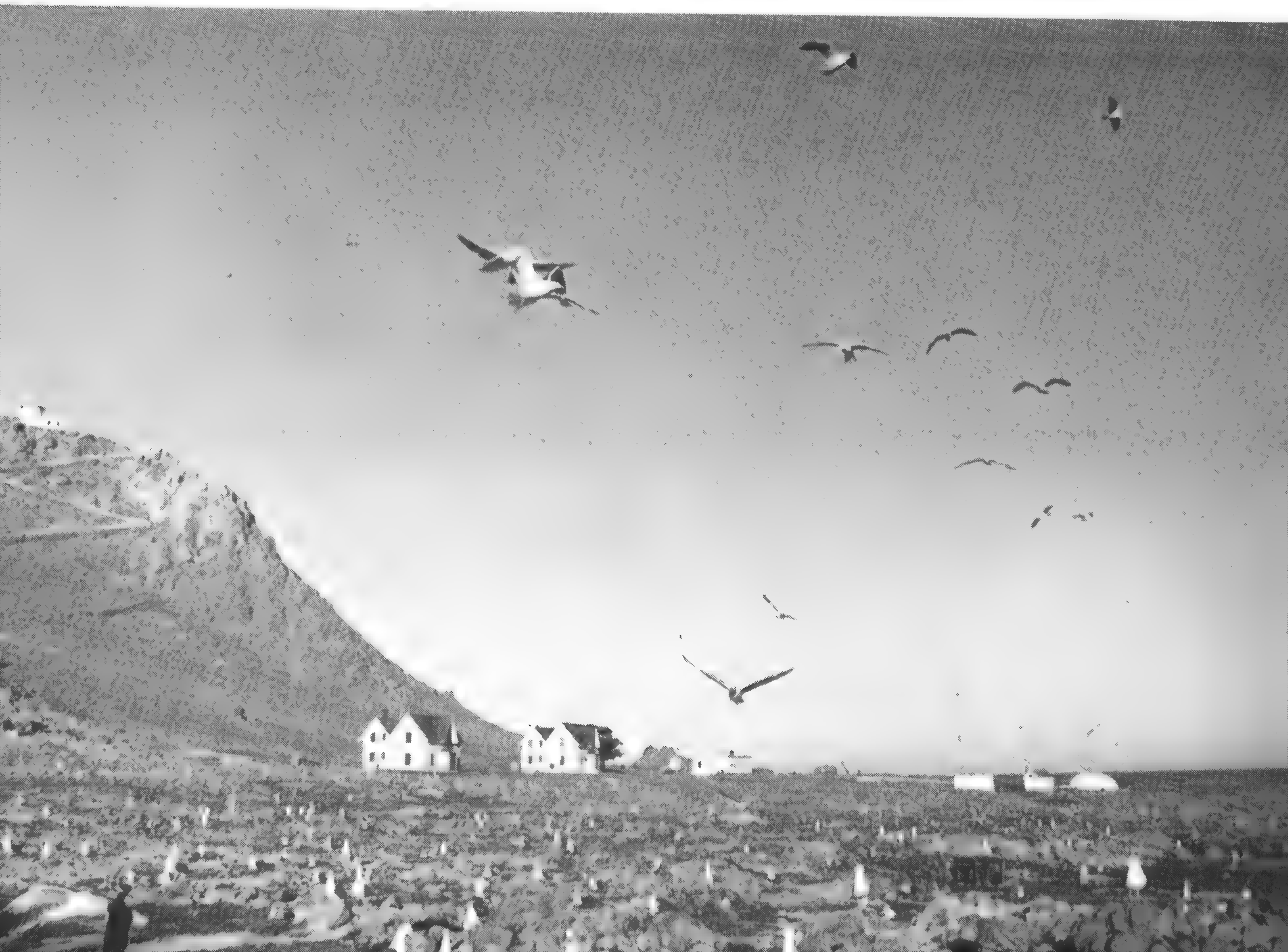


Figure 11. A summary of the annual cycles of island visitation, molt, and nesting in the two storm petrels at the Farallones. For reference, we include the annual cycle of change in plankton abundance in waters of the California Current offshore from central California (drawn after Bolin and Abbot, 1963).

discussed as strategies for avoiding large predatory birds (see Lack, 1968). And studies at Antarctic islands (Beck and Brown, 1972) and the Galapagos (Harris, 1969) have indicated that predation can greatly affect the habits of storm petrels in other ways, too. Such studies elsewhere, however, have not detected the effects we shall now describe for the Farallon species. Conditions, of course, vary from one breeding population to another.

The storm petrels on South Farallon nest mostly on the south-facing talus slope of Lighthouse Hill and on the flat area abutting the base of the hill to the south. This is the only area on the island where large gulls do not nest (22,000 breeding gulls in all; Ainley and Lewis, *in press*); and gull density on the periphery of this area is much lower than elsewhere (Figure 12). Thus, by nesting in this area, petrels largely avoid contact with gulls. This seems to be a positive response to low density of gulls rather than a coincidence, because suitable terrain for petrel nesting occurs elsewhere on the island. On some small islands near the California-Oregon border, where Leach's Storm Petrels nest within Western Gull colonies, Osborne (1971) detected a much higher mortality. He found 220 petrels in pellets during one year, which, out of an estimated population of 7,800 storm petrels there, represents more than three times the mortality due to gull predation at the Farallones. By segregating their nesting area from that of gulls, storm petrels on the Farallones reduce predation.

Figure 12. The densest storm petrel nesting area is the talus slope of the hill. Note that no gulls nest in that area but that elsewhere gulls nest in dense concentration. This photograph was taken in late May by Ian C. Tait.



Gull predation also seems to affect the timing of breeding by storm petrels on the Farallones. To be sure, the primary factor determining the breeding time is probably the same as for many other seabird populations: it is timed so that food is at a maximum for chicks and fledglings (Beck, 1970; Lack, 1954; Perrins, 1966). In addition to the two storm petrels, five other species of marine birds nesting at the Farallones feed mostly on fish and squid: the Western Gull, Brandt's Cormorant (*Phalacrocorax penicillatus*), Common Murre (*Uria aalge*), Pigeon Guillemot (*Cepphus columba*), and Tufted Puffin (*Lunda cirrhata*). The eggs of these species hatch at the same time of year, usually about three weeks prior to the hatching of storm petrel eggs. This disparity suggests that another factor modifies the primary one for storm petrels. Young storm petrels begin to fledge after almost all other species have left the island, the gulls being among the last to leave. Figure 13 describes the island occupation by the gulls and should be compared with the fledging time of the petrels shown in Figure 11.

In central California, surface waters are most productive in terms of plankton biomass and volume during May to July and are least productive from September to January (Bolin and Abbott, 1963; Smith, 1971; see Figure 11). The young of most species must grow and fledge before food becomes too limited. Because storm petrels and other Procellariiformes have slower growth rates (reviewed by Lack, 1968; Ricklefs, 1968) and possibly lower metabolic rates (Warham, 1971), however, food demand per individual may not be as high as in other birds. If they do not forfeit a significant degree of breeding success by delaying nesting, the advantage gained in avoiding gull predation may outweigh any pressures for earlier fledging. At the breeding grounds, storm petrels are no match for gulls, except under the protective cloak of darkness. This is even more true for fledglings, which are clumsy, disoriented, and naive. As an example, during walks from one building to another on autumn nights, we picked up 20 or so fledglings

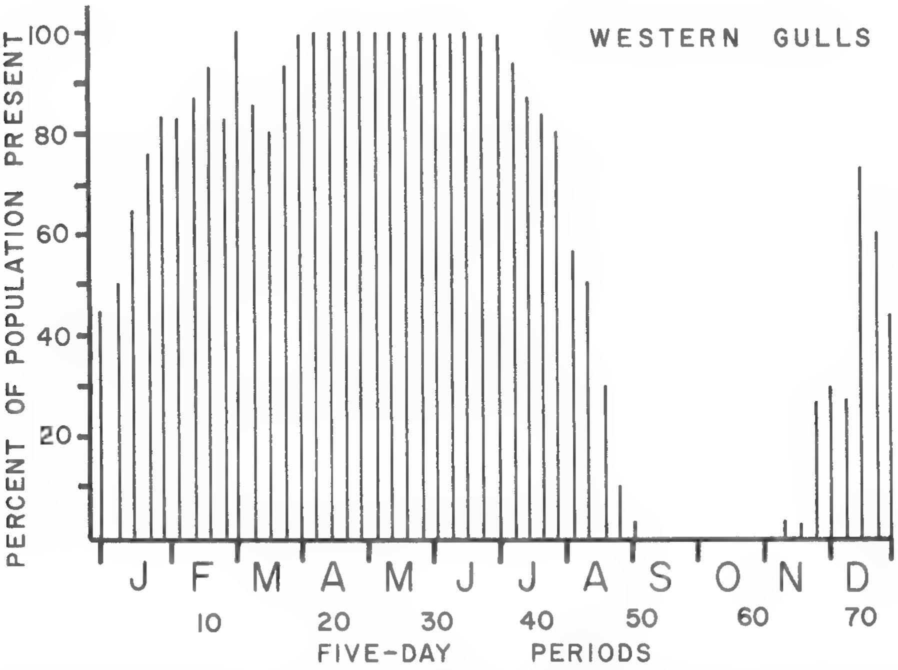


Figure 13. The annual pattern of island occupation by Western Gulls, important predators of storm petrels at the Farallones. Data were gathered during 1971 and 1972 by censusing gulls in three plots several times every day.

found sitting on the ground. This rarely occurred with adults unless they were injured, for they seldom sit quietly in the open above ground. By delaying egg-laying a few weeks and adding the time of this delay to the rather long growth period, storm petrels on the Farallones time their breeding so that the young fledge when no gulls are present. In this way, a potentially important factor in fledgling mortality is minimized.

Summary

Ashy and Leach's Storm Petrels (*Oceanodroma leucorhoa* and *O. homochroa*) were studied intensively for one year at South Farallon Island, California. Supplementary information was gathered in other years. Prior to study, the two species appeared quite similar in both morphology and biology. A comparison of several aspects in their life histories, however, showed *leucorhoa* to be a highly mobile, open ocean species that spends much time away from the island, and *homochroa* to be a rather sedentary, short-ranging species. Leach's Storm Petrel fed and wintered far from the island, which it visited for only seven months each year. This species arrived late at night, had a highly synchronous egg-laying, and overlapped molt with breeding to a minimal degree. The Ashy Storm Petrel, in contrast, fed close to the island, visited it almost the entire year, arrived each night soon after darkness fell, had an extended period of egg-laying, and overlapped molt with the pre-egg and nesting periods quite extensively. Leach's Storm Petrels lost weight over the course of the nesting cycle at a much faster rate and to a greater degree than did Ashy Storm Petrels. This was in spite of a lower wing loading in Leach's Storm Petrel, probably allowing them less energy expenditure per unit distance traveled. We hypothesized that *leucorhoa*, compared to *homochroa*, was over-extending itself a bit by breeding at the Farallones. Some other life-history patterns that the two species held in common — choice of nesting habitat, nocturnal island activity, and similar timing of breeding — are probably related to predation at their nesting grounds.

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Red-billed Helmet Shrike, *Sigmodus retzii*. Painting by Donald L. Malick in Botswana, Africa.

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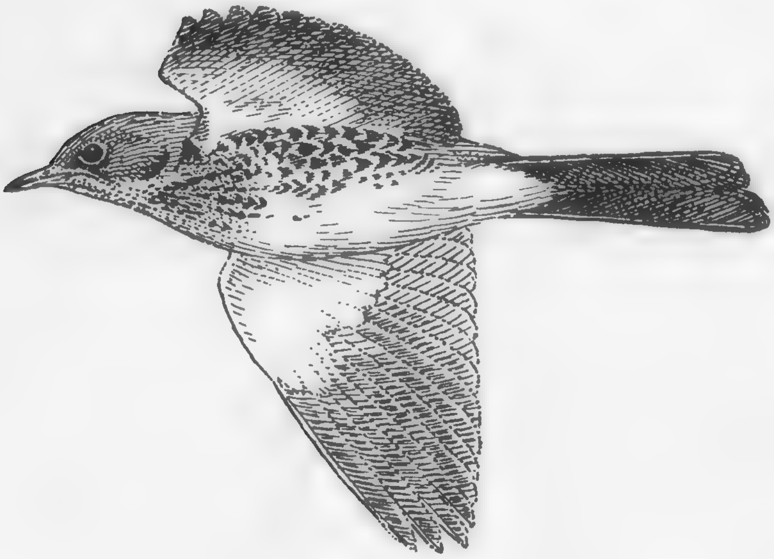

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Red-shouldered Hawk, *Buteo lineatus*. Drawing by Ted Lewin.

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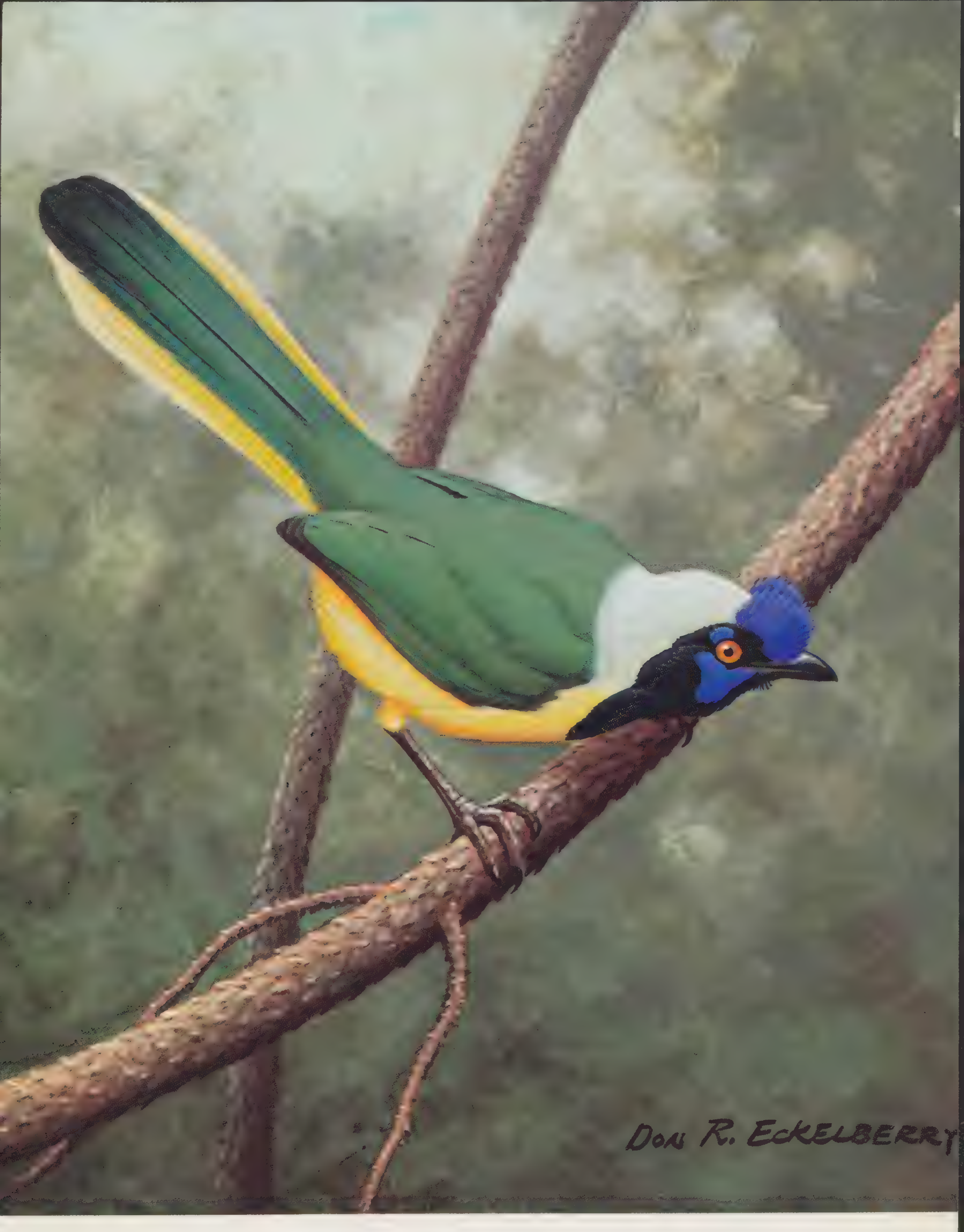


Green Jay, *Cyanocorax yncas.* Painting by Don R. Eckelberry.

THE SOCIAL SYSTEM OF THE GREEN JAY IN COLOMBIA

Humberto Alvarez

Photographs by the author

Field studies have shown that the New World jays (Corvidae, subfamily Garrulinae) encompass a wide variety of social organizations and breeding systems, ranging from territoriality by breeding pairs in the Blue Jay, *Cyanocitta cristata* (Hardy, 1961), to highly integrated cooperative breeding systems in the Mexican Jay, *Aphelocoma ultramarina* (Brown, 1963, 1970), the White-tipped Brown Jay, *Psilorhinus mexicanus* (Skutch, 1960), and the Tufted Jay, *Cyanocorax dickeyi* (Crossin, 1967), among others, and to colonialism in the Piñon Jay, *Gymnorhinus cyanocephalus* (Balda and Bateman, 1971, 1972). Brown (1974) summarized the known social systems in the subfamily, and analyzed their implications from both evolutionary and ecological viewpoints.

On the other hand, basic life histories of many species of the New World Garrulinae remain unknown.

Among the neotropical jays, the Green Jay *(Cyanocorax yncas)* occurs most widely and is rather common throughout its distribution, ranging south of the Rio Grande to north central Honduras (Blake, 1965; Monroe, 1968) and along the Andean ranges in eastern Ecuador, eastern and central Peru, northern Bolivia, Colombia, and Venezuela (Meyer de Schauensee, 1966). Thus, the species occupies a disjunct range.

In South America, the Green Jay is primarily a montane species, rarely if ever ranging below 1,000 meters above sea level (Chapman, 1917, 1921, 1926). The Green Jay occupies a wide variety of habitats, from dense thickets along watercourses and tall second-growth forests in the lowlands, to pine-oak associations and open areas of cloud forest higher in the mountains (Monroe, 1968; Russell, 1964).

Otherwise, the data on the Green Jay remain restricted to a few breeding records (Rowley, 1966; Russell, 1964), and to the breeding of a Mexican pair in captivity (Roles, 1971).

Observations I had made on the Green Jay in Colombia suggested a rather cohesive flock organization and communal defense of the nests by the flocks. The habitat of the species in most of its Colombian range has been drastically modified as the subtropical and montane forests have been extensively cleared for agricultural purposes. In several regions, also, the original forest has been artificially replaced by extensive, homogeneous coniferous forests, mainly for watershed protection and the production of pulp.

This little-known neotropical jay thus offered a promising subject for studies related to social organization and the adaptation of a species to a rapidly changing habitat.

The Study Area

I studied the Green Jay in the Central Cordillera of the Andes in northern Colombia at approximately 6° 21' 46" N, 75° 36' 18" W, between 2,425 and 2,500 meters above sea level. The locality was about 27 kilometers northwest of the city of Medellin, on the route to the town of San Pedro. The flocks under observation covered an area of roughly five square kilometers. I visited several other nearby localities for short term observations.

Espinal (1964) classified the region of the study area as "lower montane humid forest" in Holdridge's system. The average annual rainfall for a 23-year period is 1,712.9 millimeters. From September 1972 to August 1973 the rainfall was 1,675.7 mm (See Figure 9). A marked dry season from December through March produces less than 18 percent of the annual average. During the dry season of 1972-1973, 223.3 mm of rain fell, only 7.5 percent of the rainfall for the 12-month period. Frosts occur frequently in the early morning during the dry season. No temperature data were available.

Dominant features of the topography are the deep, narrow valleys carved by small creeks, and the high, steep intervening ridges. The high rainfall and the underlying granitic rock, readily weathered and eroded, are responsible for the strongly dissected landscape.

Dairy farms (Figure 1) occupy about 60 percent of the study area. Occasionally, small extensions of the grasslands are plowed for growing potatoes, and afterwards rotated with corn and beans. Small patches and rows of foreign cypress *(Cupressus lusitanica)* are prominent elsewhere. Cypresses are planted along the dryer ridges, in fences, and as wind barriers. Very few native trees are left on the pasture lands, and most of them are hardy second-growth species *(Vismia guianensis, Myrcia popayanensis, Tibouchina lepidota).*

Dense secondary forests grow only in narrow strips along the watercourses, and they represent several sucessional stages, with varying degrees of interference by cattle and fire-wood gatherers. Only a few individuals of the oak *Quercus humboldtii* have been left from the original forest.

In the northern section of the study area (about 40 percent), formed by the slopes of "La Garcia" reservoir, the secondary forest is further reduced. Most of the vegetation here consists of even aged, homogeneous plantations of *Pinus elliottii* and *P. patula* (Figure 2). Gum trees, *Eucalyptus viminalis* and *E. globulus,* have been planted along with *Acacia melanoxylon, Pinus radiata,* and cypresses, but to a lesser extent and occur as leftovers of earlier reforestation experiments.

Methods

From early September 1972 to the end of September 1973, I followed four flocks of jays, plotting their locations and travel routes on a topographical map (scale 1:5,000 with contours every 25 meters). A grid of 50-meter squares made it possible for the position of any one flock being observed to be described by referring to an x-y coordinate system.

I spent 3,150 hours in the field, and concentrated on the two flocks that ranged nearest to my camp. At least one day per week was devoted to the other two flocks. I made most of the general observations with binoculars, and dictated notes into a portable tape recorder. I observed nests with a 20x-30x spotting scope from blinds.

I captured and color-banded 20 jays throughout the study period. Each bird received one numbered aluminum ring, and five celluloid, coil type, colored bands. Young at the nest were fitted with only four rings, one of them of aluminum. The bands were coded in such a way that the reading of the three bands on any one leg would provide positive identification. The bands were cemented shut with Aero-cement, and none were lost during the study period.

I captured thirteen of the birds with mist nets placed on the usual routes of the flocks and on small corn plots. As the jays moved rather slowly through the vegetation, and did not make long, fast flights, they usually saw the nets and avoided them. It was necessary to devote a great amount of time to setting the nets, and to constantly changing their location until captures were achieved. I marked four birds as nestlings, and captured and banded three more within the first days after they fledged. I also tried a variety of wire mesh traps baited with pieces of bread and whole corn ears; these traps produced no results, as the jays became very wary of any foreign objects and would not even come close to the traps.

I could sex Green Jays reliably only by their behavior at the nest, as there are no readily apparent sexual differences in plumage or size. By following the technique described by Risser (1971), I attempted to sex five birds by laparotomies. However, the size of the gonads was so reduced in all cases that sex determination under field conditions was extremely unreliable, and I finally abandoned this method.

I measured the culmen, right wing, right tarsus, tail, and nasal tuft of each captured jay. I also made notes on molting, on conspicuous features of coloration, and on the presence of incubation patches and cloacal protuberances. I obtained the weights of 14 jays by means of 100-gram and 300-gram Pesola spring scales.

Three jays from one of the unmarked flocks under study, and four from a nearby region, were collected and their stomach contents preserved for identification and analysis.

Flocking

Movements

Besides its brightly colored plumage, gregariousness is one of the first qualities of the Green Jay that even a casual observer is likely to notice. Upon meeting a flock, one first notices the loud, discordant alarm calls, and then the yellow, black, and green plumage as the jays fly away. Even though I often saw only isolated individuals, the presence of the flock was apparent by the exchange of contact calls among the members.

The flocks, when undisturbed, progressed slowly through the foliage along fronts of variable width, rarely more than 50 meters and moved up and down in the available strata of vegetation. The distance between individuals varied from bodily contact of twos and threes during mid-day resting spells to 15 or 20 meters during periods of more active foraging.

Frequently, one or more jays moved forward, leaving the rest of the flock up to 35 or 40 meters behind, or else laggards fell back and became temporarily isolated. In any case, the separation did not last more than a few minutes. In the few instances when I was able to remain unnoticed by the jays while standing quietly in their paths of movement, I could see all the individuals within a radius of less than 30 meters as they passed by.

While foraging or resting, the Green Jays were relatively silent, occasionally uttering short series of subdued notes, probably as a means of keeping in contact. It was possible to approach an active flock closely in dense secondary vegetation without noticing them. Whenever an individual lost contact with the other members of the flock, it climbed to a convenient lookout and delivered loud calls until the other jays responded with similar calls.

The Green Jays were particularly shy of humans, and once they discovered me, they called in alarm and rapidly fled. The wide front was broken as the jays flew out of sight in a narrow line. Cautious movements or even complete stillness were of no avail, and I did not record any relaxation of their shyness, even after I had followed the same flock for several consecutive days. They became even more wary after capturing and handling.

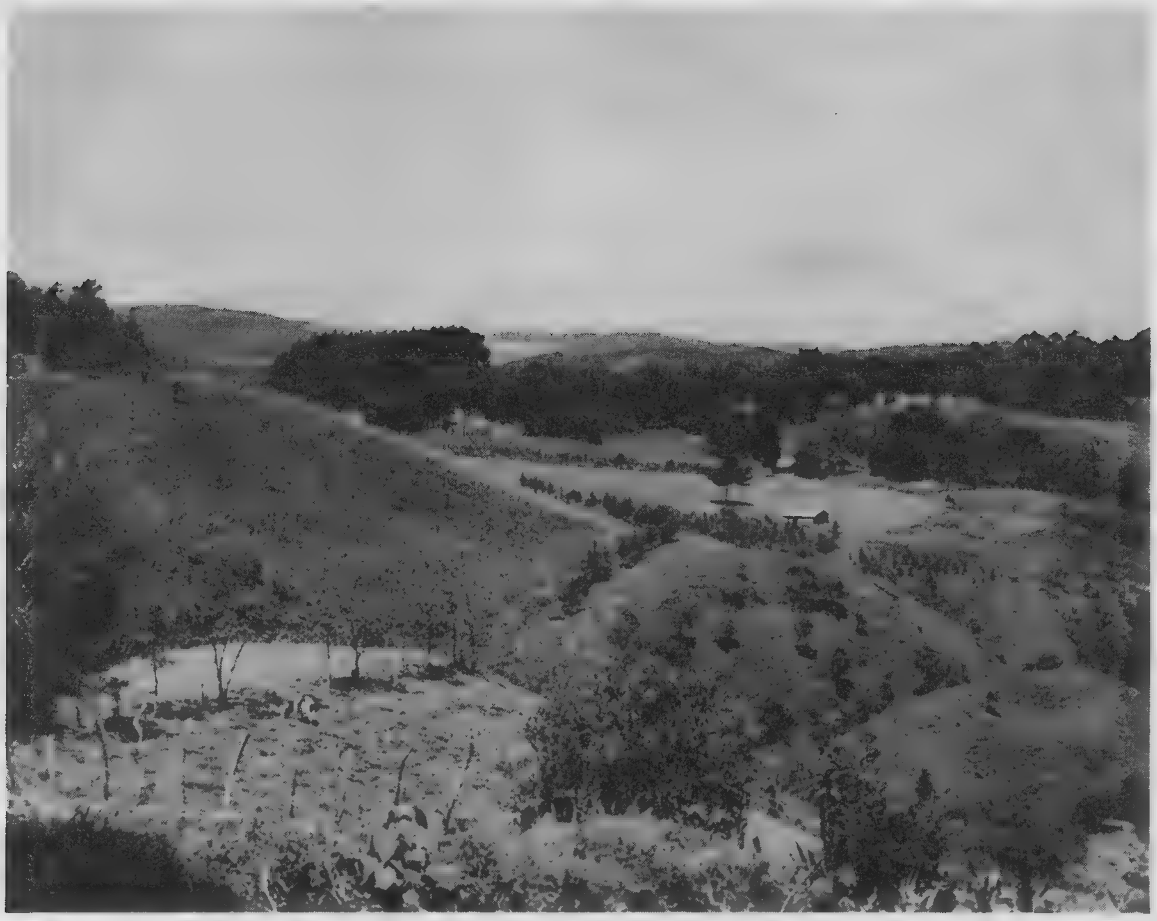


Figure 1. Dairy farms on the southwestern section of the study area. Flocks of Green Jays foraged along the cypress rows and on the scattered trees in the pastures.

Green Jays showed a definite aversion to open spaces of more than 50 to 60 meters. I saw only one case of a flock flying across an open area of about 75 meters when hard pressed to do so by the resident flock defending its territory. In the territory of Flock 2, there existed a large meadow about 150 meters across. Very often this foraging flock became temporarily divided into two sub-groups that surrounded the meadow, and then constantly exchanged loud contact calls. At no time did I see any jays flying across the pasture; instead, the two sub-groups always retraced their routes and reunited near the site at which they had originally split.

The avoidance of large open spaces resulted in well defined routes of travel, usually following the most densely vegetated watercourses and wind barriers along the ridges. This was particularly true of Flocks 1 and 3. The territories of Flocks 2 and 4 contained vast stretches of dense, coniferous forests, and consequently their travel routes were less predictable.

Flights across large open spaces always started from the tallest available tree, to the top of which the jays climbed before launching a downward flight with intermittent flapping, similar to the undulating flight of woodpeckers. The long tail opens and closes, flashing the bright yellow rectrices. Of 92 such flights, I witnessed only 27 (29 percent) occurring with another jay in the air at the same time. Even then, the leading jay was always close to the other side of the clearing when the following one started. Usually, one bird waited before taking off until the preceding one reached the patch of forest toward which it was flying, even though two or more birds were at the starting point.

Flock Size and Structure

I readily ascertained the number of jays in a flock by counting them as they flew across open spaces in the manner described above, and by following the flock for several hours in order to account for temporary splittings. The only sources of error could be females at the nest at the time of counting, and the coincidental presence of two or more flocks in one place. However, the behavioral interactions that invariably followed flock encounters left no doubts that several flocks were involved. Table 1 summarizes the data on flock size and structure.

By studying differences in plumage related to age, it was possible for me to distinguish immatures from adults in the field. Immature Green Jays had a reduced fronto-nasal tuft and displayed a nuchal band of blue feathers (Figure 3). In adults, the fronto-nasal tuft was well developed and the nape was yellowish white, without blue feathers (Figure 4). Figure 5 shows the changes in numbers and age structure throughout the study period in the four flocks under observation.

The changes in size and structure for the entire population are shown in Figure 6. The plottings correspond to the state of the population at the end of each month.

The two banded flocks maintained fixed memberships throughout the year, and I could not detect any exchange of individuals between them, even though these two flocks mixed together during territorial encounters and shared a part of their ranges. However, as I describe more fully later, some jays moved between two factions during the early stages in the splitting of Flock 1.

Six jays disappeared from the study area between September 1972 and

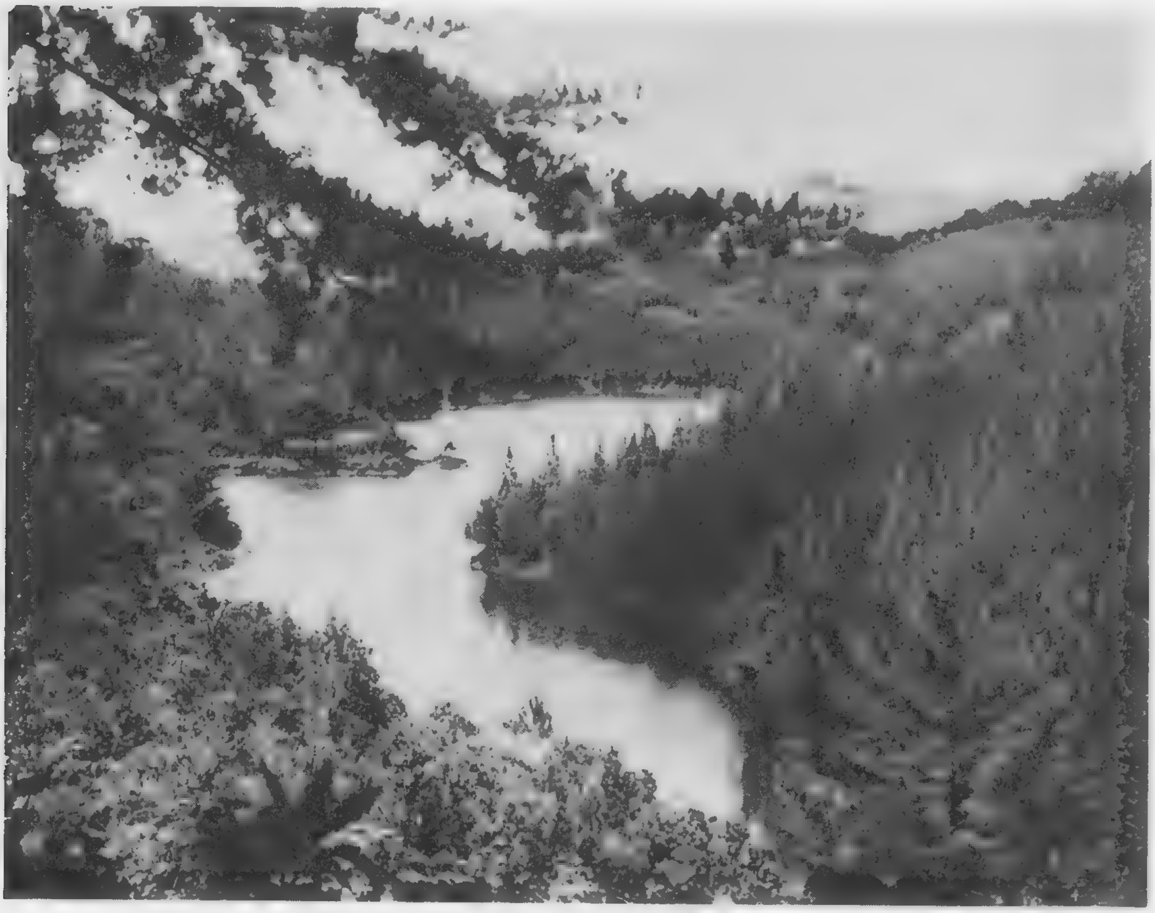


Figure 2. Pine plantations on the slopes of "La Garcia" Reservoir, northern section of the study area.

February 1973 (Figure 5). Four of them (66.6 percent) were immatures. As isolated individuals leaving their territories would have been difficult to detect, emigration remains a possible cause for the losses recorded. However, I never found any of the two missing banded jays of Flock 2 either by themselves in one of the areas adjacent to their original territory, or attached to one of the neighboring flocks. Predation was also a likely cause for those casualties, but I could not gather any evidence on actual predation of Green Jays out of the nest.

Origin of New Flocks

New flocks seem to originate by permanent splitting of old ones. Flock 1 went through a gradual process of division, but unfortunately I was unable to document the establishment of one of the parts after its segregation. By 15 April 1973, and after the failure of their first nest, Flock 1 started building a second nest. At that time the flock was composed of seven adult jays (Female XRM, Male "Long Crest," XYB, XYM, XMY, XMB, and "Blue Head"). However, I saw only three of them (XRM, Long Crest, and XYM, from now on referred to as Flock 1A) involved in activities clearly related to this second nest, while the others lagged behind and never approached the nest tree.

The second nest was abandoned half-built, and by 1 May a third nest was finished by Flock 1A. This flock had been away from the other jays referred to as Flock 1B, since 17 April, when the former changed their roosting place to an unknown location. From the first days of May, probably from the beginning of the incubation period, Flock 1A roosted near the nest site, while Flock 1B retained the original roost. None of the members of Flock 1B were ever seen around the third nest.

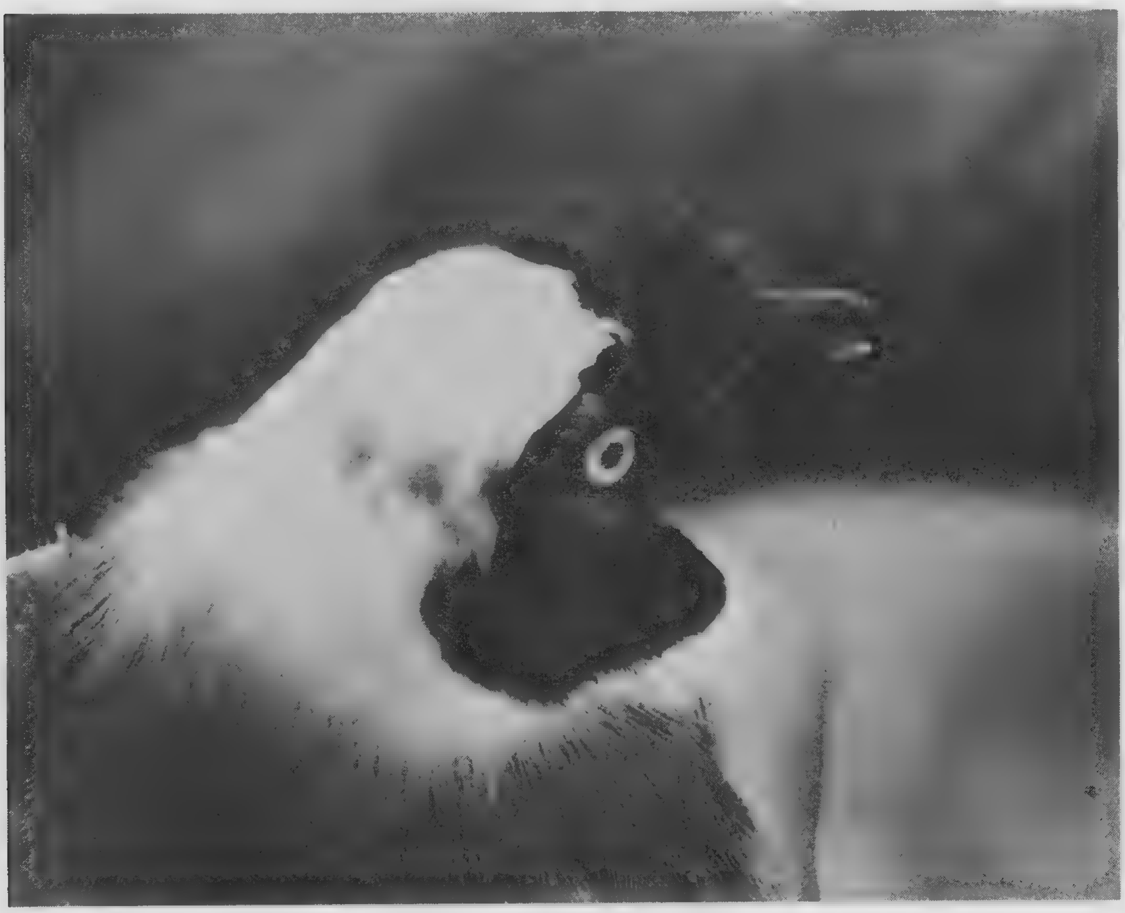


Figure 3. Immature Green Jay showing reduced fronto-nasal tuft and nuchal band of blue feathers.

I became fully aware of the splitting of the original flock on 19 June. As I tried to capture one of the young that fledged on that morning from Nest 3, the loud scolding calls given by the parents and the one helper attracted all four members of Flock 1B, and a typical territorial confrontation ensued between Flocks 1A and 1B. About 90 seconds later the interlopers fled, closely chased by the resident faction.

During the following days, I saw no more territorial encounters, but the two factions remained apart and kept separate dormitories. On 28 June, Long Crest, the mated male of Flock 1A, was seen courtship-feeding XMB of Flock 1B in the immediate vicinity of the three fledglings. Long Crest left following XMB, and stopped bringing food to the young. From this date on, I saw Long Crest regularly along with the jays of Flock 1B.

On 29 June, XYB transferred to Flock 1A, and although it never brought food to the young, XYB followed the flock regularly, and participated in scolding. On 2 July, Flock 1B moved its dormitory to a patch of dense secondary forest about 150 meters from the original one.

Until 15 July Flocks 1A and 1B shared the original territory, but remained clearly segregated. On 9 July, XMB also had transferred to Flock 1A, leaving Long Crest, XMY, and Blue Head as members of Flock 1B. Careful searches conducted from 16 to 20 July failed to reveal the new range of this flock, and I never saw them again. Flock 1A had moved on 17 July to the original roosting place, the same that was vacated on 29 June by the other faction, and kept the same territory without noticeable modifications of the boundaries. The final composition of Flock 1A was, then, four adults (XRM, XYM, XYB, and XMB), and one juvenile (XYR), the only survivor from the clutch of Nest 3.

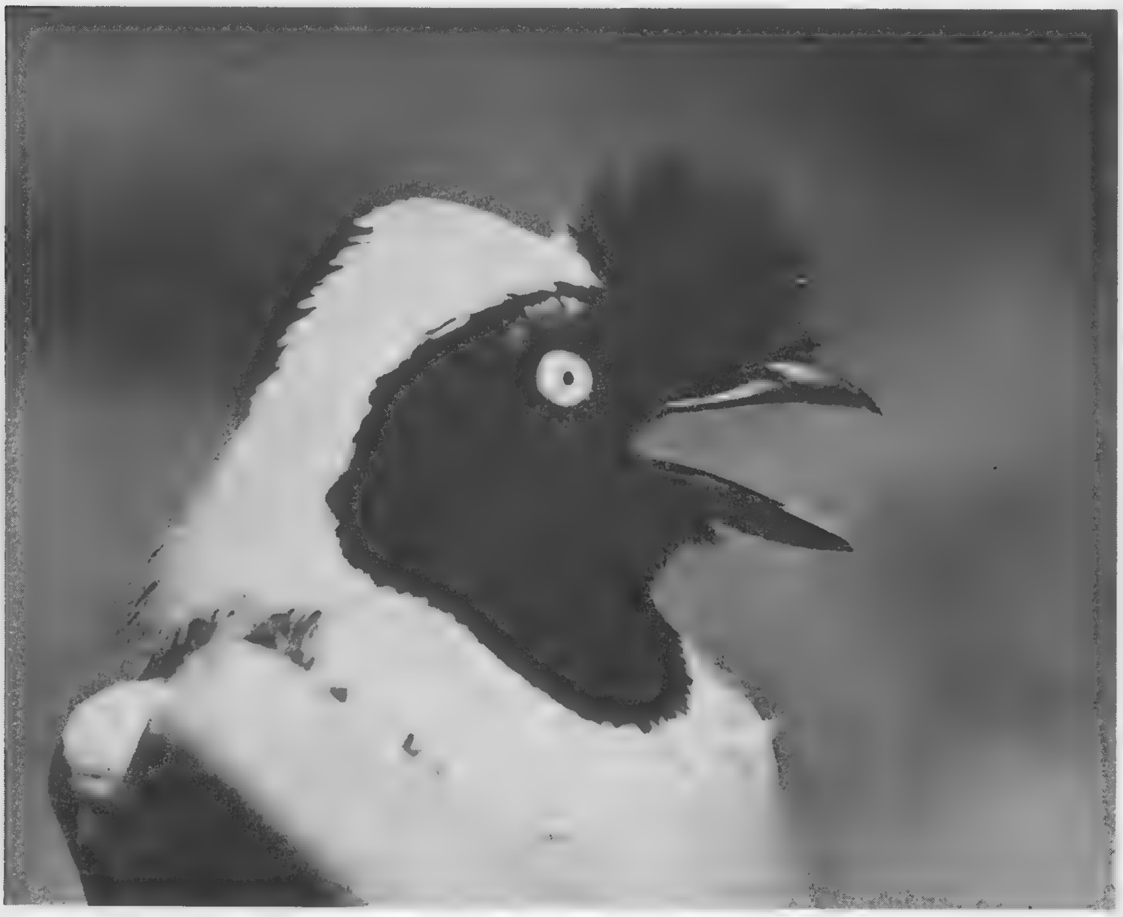


Figure 4. Breeding male. The fronto-nasal tuft is well developed, and the nape is yellowish white without blue feathers.

TABLE 1

Size and Age Structure of Green Jay Flocks

Locality	*Size*	*Adults*	*Immatures*	*Source*
San Pedro, Antioquia	5	2+	1+	This study[1]
Piedras Blancas, Antioquia	6	4	2	This study[1]
Santa Helena, Antioquia	8	3+	2+	This study[1]
Granada, Antioquia	4	—	—	This study[1]
Study Area, Flock 1	8	4	4	This study[1]
Study Area, Flock 2	8	4	4	This study[1]
Study Area, Flock 3	5	3	2	This study[1]
Study Area, Flock 4	6	4	2	This study[1]
Rancho Grande, Venezuela	"6-10"	—	—	Wetmore, 1939
La Aguadita, Cundinamarca, Colombia	"up to 5"	—	—	Olivares, 1969

[1] Average size of the nine flocks in this study was 6.1 jays. The smallest flock contained four birds, the largest eight birds.

Territoriality

Territorial Boundaries

All four flocks under observation maintained territories throughout the year. I defined the boundaries of these defended areas by the movements of the jays in their daily activities, as well as by the territorial interactions between flocks with adjacent domains (Figure 7).

Territorial boundaries usually coincided with topographic features such as ridges, roads, creeks, and the borders of pastures. The shores of the reservoir in the northern half of the study area served as boundaries for the territories of Flocks 2, 3, and 4. In some areas, however, the borders were rather ill-defined, and I determined boundaries here by recording the few territorial encounters I witnessed along those tracts. This was the case for the common boundary between the territories of Flocks 2 and 3.

The territories of Flocks 1, 2, and 3 overlapped slightly in an area devoted to small plots of corn, beans, and peas. The area shared by the three flocks, about 0.75 hectares, was the site of a number of territorial encounters.

Flocks 3 and 4 had a common boundary along the densely forested outlet of "La Garcia" reservoir; but I never recorded an inter-flock encounter even though flocks came within hearing distance of each other several times.

Size and Composition of Territories

No important changes took place in territorial boundaries, even though abundant sources of food became available in unoccupied ranges within short distances from the boundaries. At less than 150 meters from the western boundary of Flock 2's territory, there existed a corn plot of about three hectares that no jays visited. The intervening ground was a steep slope devoid of trees and crossed by a road.

The same flock slightly extended its territory to include a small corn plot unoccupied by other jays. The plot was some 25 meters from the original boundary across a road edged by trees. The presence of trees for intermediate stops and/or prospective cover, along with the distance of open ground to be crossed, seems to determine the accessibility of an area for the jays.

Between 15 April and 1 May, Flock 1 extended its range to a section of about five hectares that appears in Figure 7 as a southeastern projection of the territory. In this area the flock built their second nest of the season, and frequented this territorial extension only while constructing the nest. They abandoned it as soon as they stopped building, moving elsewhere to start a third nest.

The four territories comprised several types of vegetation in varying proportions. The extension of the territories and the proportion of each vegetation type could be accurately measured for Flocks 1, 2, and 3 (Figure 8).

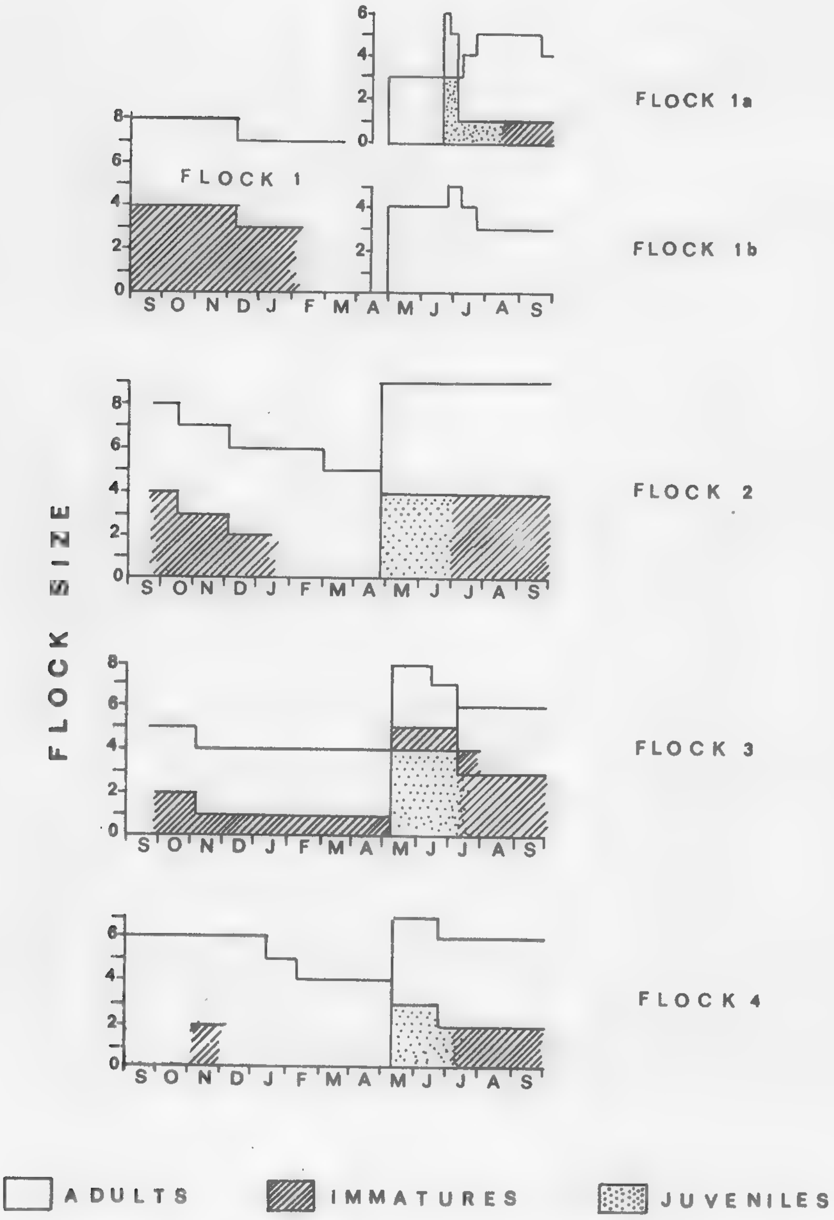


Figure 5. Changes in numbers and age structure in four flocks of Green Jays throughout the study period (September 1972 to September 1973). I considered any given jay as no longer a member of the flock on the first date that I noticed it was missing. The juveniles are considered as members of the flock, and thus entered on the graph, on their dates of fledging. Open areas represent adults; diagonal lines indicate immatures; stippled areas represent juveniles.

Territorial Defense

Resident flocks actively defended territories at all times. I made detailed notes on eleven encounters. Actual trespassing of occupied territories was relatively rare, and I only recorded two instances of encounters well inside the territory of Flock 1, following incursions by Flock 3. All other encounters occurred at the boundaries and in the small area common to the three flocks.

Typically, upon hearing the calls of a foreign flock near the boundaries, the resident jays moved rapidly to meet the interlopers, calling loudly in alarm. The actual encounter started with the clustering of jays of both flocks in one or two shrubs or trees. The jays often distributed themselves in twos and threes close together, several of them bobbing simultaneously while bill-snapping and uttering the rattle calls that usually accompanied this display. Supplanting attacks, often in a rapid series of two or three by the same individuals, occurred in the same tree by members of both flocks, and resulted in short circular chases. Less frequently, but seen regularly, two contestants clashed and fluttered to the ground grasping each other's feet. Once on the ground they separated and faced each other, a few inches apart, with wings dropped, bills pointed forward, and neck feathers ruffled. Several other jays followed the fighters to the ground or to low branches nearby. One of the contestants eventually chased the other one back to a tree. After another one or two of these fights, with intermediate spells of clustering, bobbing, and supplanting attacks, the intruding flock retired, closely followed to the borders by the residents. I saw no instances of chases proceeding beyond the territorial boundary.

Sometimes the interaction described above was avoided when the intruders flew away at the approach of the resident flock.

On occasion, jays traveled long distances to defend their territories. On 16 February 1973, Flock 1 was foraging well inside its territory when Flock 2 came to the cypress grove, some 200 to 250 meters away from Flock 1's original

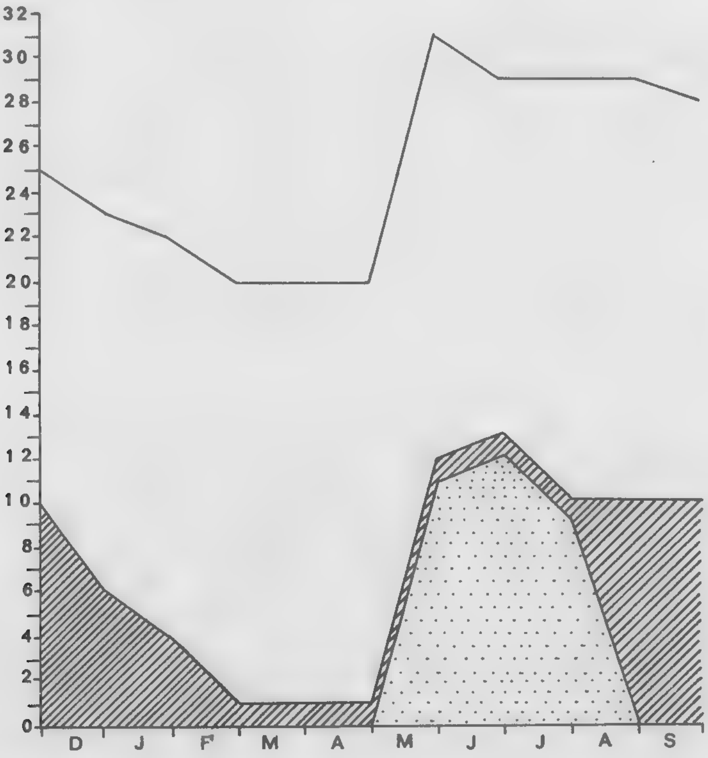


Figure 6. Changes in numbers and age structure in a population of Green Jays (Flocks 1 to 4) from December 1972 to September 1973. Open areas represent adults; diagonal lines indicate immatures; stippled areas represent juveniles.

location. At the approach of the residents, Flock 2 advanced an additional 50 meters inside the territory, an encounter followed, and Flock 2 retreated.

On 5 November 1973, in an attempt to attract the jays of Flock 1 to the mist nets, I played back from a tape recorder an assortment of vocalizations of Green Jays, including the loud long distance calls. At that moment the jays were at least 300 meters away on the facing hillside. Within four minutes, all seven jays had assembled less than 20 meters from the recorder. Repeated playbacks had no effect in attracting the birds any closer, and they left after two or three minutes.

The rapidity with which all the events happened during territorial encounters, plus the fact that I had to keep my distance to avoid disturbing the jays, did not permit me to ascertain the roles of individual flock-members during these confrontations. My overall impression, based more on the numbers of jays involved than on individual identification of the contestants, is that all members of the flocks participated in the encounters except, of course, newly fledged young.

Interspecific Interactions

I did not see Green Jays participating in mixed species flocks. Only individuals, or pairs at most, of the Golden-olive Woodpecker *(Piculus rubiginosus)* occasionally followed and foraged along with flocks of Green Jays, for periods that ranged from five minutes to about one hour. On two of these occasions, one woodpecker came several times within 30 cm of one of the jays without eliciting any visible reaction by the jay. When I approached, the jays started to call in alarm, while the woodpecker kept searching for food in the bark crevices of a *Tibouchina* tree, seemingly undisturbed by my proximity. However, when the jay that was closest to the woodpecker flew away, the latter followed immediately and alighted in the same tree as two of the jays.

A pair of Golden-olive Woodpeckers roosted for at least three months in the same patch of dense secondary growth as the jays of Flock 1. Late in the afternoon, when the jays entered the roosting site, both woodpeckers followed them for several minutes until the jays settled down for the night. I never saw any aggressive interactions between the two species, nor any other movements that I could interpret as mutual avoidance.

Giant Cowbirds *(Scaphidura oryzivora)* showed a notorious interest in the Green Jays. From November 1972 to May 1973, I saw high-flying cowbirds in small flocks of up to four birds come down to land nearby at the sight of the jays. Then, they followed the jays for variable lengths of time up to one hour, keeping a distance and never mixing with the jays for foraging.

The reactions of the jays to the proximity of the Giant Cowbirds were variable. During the non-breeding season the followers were mostly ignored, even when they came within close distance of the jays. On 11 May 1973 a flock of four cowbirds had been following the jays of Flock 1 for about 20 minutes. One of the jays became temporarily separated from the flock, and was approached by one cowbird that came to perch in the same small shrub and less than 50 cm from the jay. The latter did not visibly react and the cowbird left the place after a few seconds.

On 3 March a flock of three cowbirds came to the same tree where the jays of Flock 2 had clustered following a territorial encounter. Immediately, three of the jays moved toward them silently, and the cowbirds moved to join Flock 3, some 50 meters away. After a few minutes, the cowbirds went after Flock 1 and followed them for nearly half an hour.

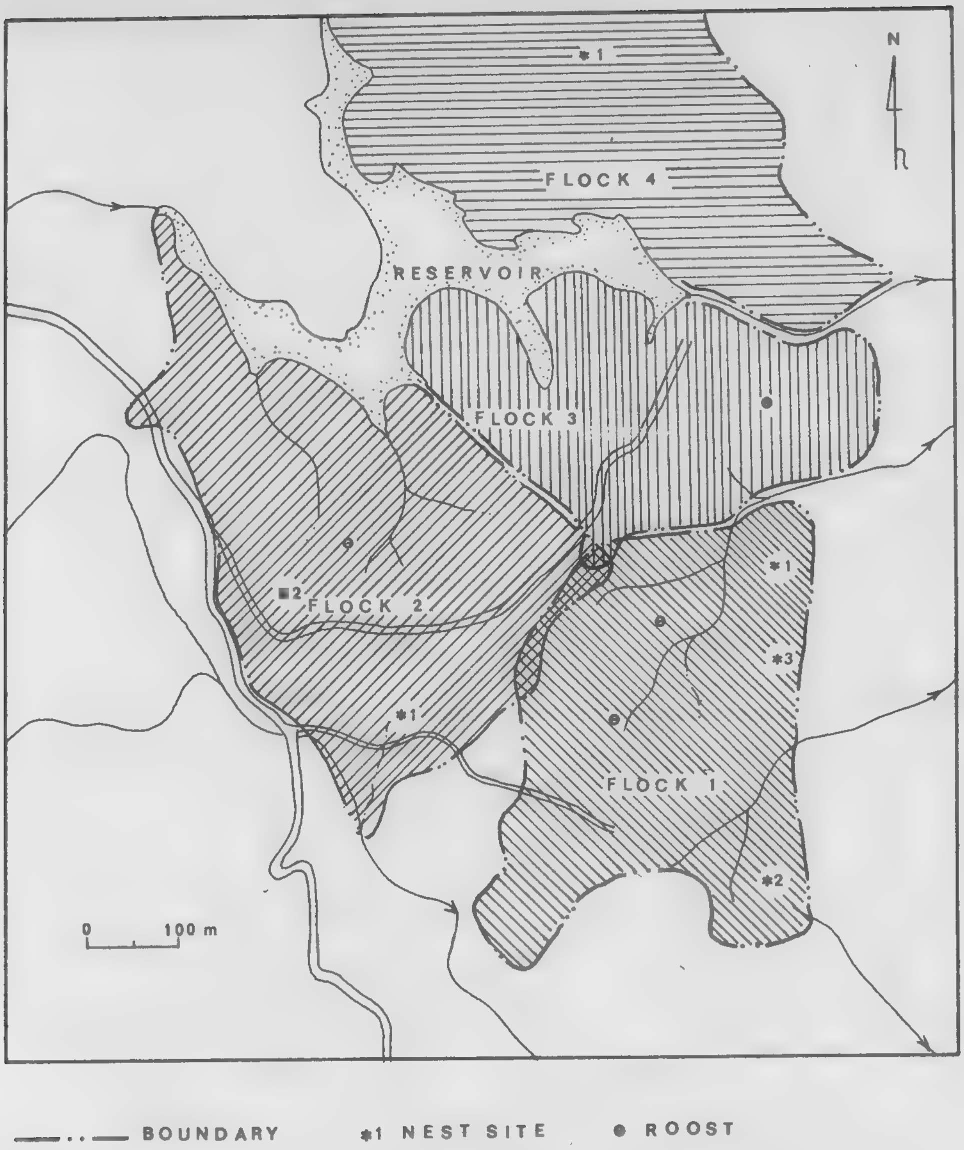


Figure 7. Territorial boundaries, nest locations, and roosting sites of four flocks of Green Jays in the study area. Nest sites are indicated by asterisks and numbers. Small circles show roosting sites.

Both the curiosity of Giant Cowbirds toward Green Jays and the intensity of the related reaction by the jays increased during the latter's breeding season. The jay invariably chased away any cowbirds that came near the active nests, sometimes as many as four jays joining in the defense. The chases were silent except for occasional rage-calls uttered by the jays.

From 31 March 1973, one day before the eggs in the second nest of Flock 2 hatched, to 24 April when the young fledged, I saw the Giant Cowbirds every day near the nest. They clearly oriented their movements toward the nest, and occasionally came to perch on the nest's supporting branches. Any jay in the vicinity of the nest attacked the cowbirds, and sometimes the female stopped brooding to go after a cowbird that came near. In spite of this, the cowbirds, as many as three at a time, came back after a while to be chased away once again.

In 106 hours of observation at the second nest of Flock 2, from 31 March to 23 April, I witnessed 17 interactions as described above, at least one in each observation period.

Robert Chipley (pers. commun.) reported two cases of young *Scaphidura* following Green Jays and begging from them. Lehmann (1960) also recorded one young Giant Cowbird being fed by a pair of Green Jays in southwestern Colombia. Although I did not see any cases of parasitism of Green Jays by cowbirds, I heard from residents of the region around my study area that the jays are occasionally seen feeding the young of a "black bird."

Among several species of raptors recorded from the study area, only the Sharp-shinned Hawk *(Accipiter striatus)* is likely to prey on Green Jays out of the nest. I saw this hawk attack the jays unsuccessfully in all nine instances that I could record in detail (Table 2).

At the sight of this hawk, or after the hawk's first attempt to make a capture, the jays usually flew close together under the densest available cover, closely followed by the hawk as it made short and fast dives through the foliage. Every time a jay was attacked, it dropped to a lower perch in time to avoid the hawk. On the other hand, every time the hawk perched, one or two jays approached and jabbed at it, either from below or above, forcing the hawk to retreat, after which as many as four or five jays went after it. As soon as the jays started to move ahead, the hawk struck again, and so on. On 10 December 1972 I counted four attacks by a hawk in a ten-minute engagement.

These back-and-forth chases went on for as long as 35 minutes, while the jays traveled distances of up to 120 meters. The interactions always ended with the Sharp-shinned Hawk giving up and flying away after an attack by the flock.

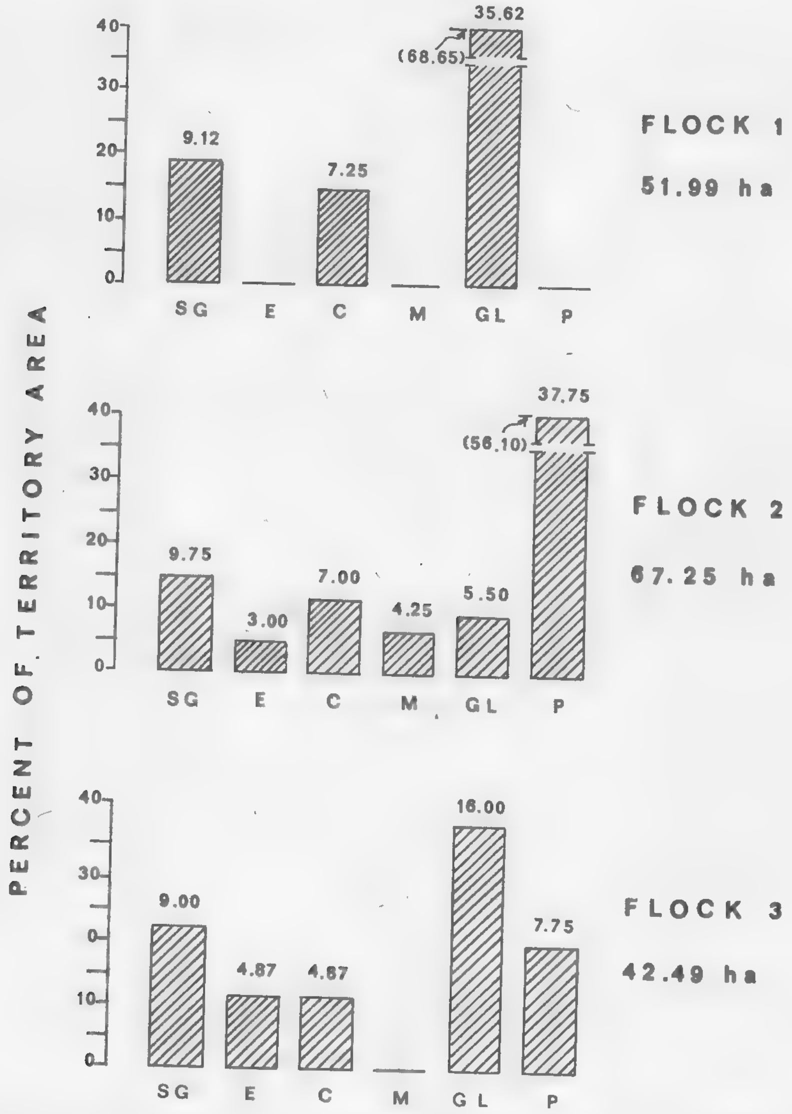


Figure 8. Extension and distribution of vegetation types in the territories of three flocks of Green Jays. SG, secondary growth; E, *Eucalyptus* spp; C, *Cupressus lusitanica;* M, meadow; GL, grassland with scattered trees; P, *Pinus* spp. Numbers on top of the bars indicate the extent of each vegetation type in hectares, and the size of the territory is given at the right hand side of each graph.

During all these interactions, it became clear that the jays were reluctant to leave their refuge, and preferred to harass the hawk instead of fleeing or dispersing. On 25 August 1973 Flock 3 had been threatened by a Sharp-shinned Hawk for about nine minutes when the jays came to the end of a row of trees along which they had been moving, separated from the nearest tree in a cypress grove by about 15 meters of open space. The jays remained in the tree for two more minutes during which the hawk tried once more, this time on an immature. The chase by the jays that followed drove the hawk out of the tree to the nearest cypress. Only then did the jays leave the tree in which they had been cornered.

Roadside Hawks *(Buteo magnirostris)* were the most abundant birds of prey in the study area, but I never saw one attacking the Green Jays. However, jays occasionally harassed these hawks by climbing to the top of a tree to force a perching hawk to flee by jabbing at it from below. The same treatment was given once to a Broad-winged Hawk *(Buteo platypterus)*.

I recorded only one case of predation on eggs of the Green Jay. On 10 April 1973 my wife was watching an unattended nest with a clutch of four eggs. After about ten minutes, a Smooth-billed Ani *(Crotophaga ani)* came to the nest tree and was chased immediately by one of the jays. However, the ani returned directly to the nest a few minutes later and pecked one of the eggs just before being attacked by the owners. The same jay went back to the nest and ate the broken egg. The next day I found the three eggs cold, and it was clear that the nest had been deserted.

Near their nests the Green Jays attacked a variety of other birds. In these cases no more than one or two jays participated, and the interactions never developed into anything beyond one or two supplanting attacks. Great Thrushes *(Turdus fuscater)*, Squirrel Cuckoos *(Piaya cayana)*, Yellow-billed Cuckoos *(Coccyzus americanus)*, and Blue-crowned Motmots *(Momotus momota)* were all harassed and driven away whenever they came into the immediate vicinity of a Green Jay's nest.

Green Jays were frequently attacked by Great Thrushes, usually in pairs, and near dense mats of low shrubs. I never was able to learn if the thrushes had nests nearby, but this at least indicates that Green Jays are recognized as predators by Great Thrushes.

Food and Foraging Behavior

Green Jays exploited a wide variety of food resources in an equally wide spectrum of habitats and substrates. As the jays moved through the vegetation, they searched for food in all the available strata, including the ground, tree trunks, and branches. Rotten stubs of branches were pecked open, probably to search for wood-boring insects. Lichen clusters were also attractive to the jays, and bromeliads became, on occasion, reservoirs of drinking water as well as sources of arthropods that took refuge at the wide bases of their leaves.

In foraging, the jays usually proceeded from the lower branches to the top of trees and shrubs, and from the trunk to the tips of even the most slender branches. I did not detect any overlap of the feeding paths between jays of a flock. Foraging jays distributed themselves along wide fronts instead of following each other along narrow paths. Although it was not rare to see two jays arriving at the same shrub or small tree, they always searched for food on separate branches. I never saw two jays in succession exploring the same branch, except on one heavily laden with fruit.

TABLE 2

Summary of Interactions Between Green Jays and Sharp-shinned Hawks

Date	*Flock*	*Duration (minutes)*	*Observations*
8 November 1972	1	16	In grassland with scattered trees, 8 jays attacked at least 3 times by the hawk. All the jays chased the hawk between attacks by the latter. After attacks, the jay imitated the hawk's calls.
18 November 1972	2	3–4	In secondary forest. After overflying the site of Nest 2 (then with 4 eggs) a hawk perched on the tip of a cypress, some 120 meters distance from the nest. Three jays climbed up the tree and jabbed at the hawk from below, causing it to climb higher. After 8-10 seconds the jays came back near the nest. One minute later, the hawk dived from its post after one jay, but missed and was chased by the same three jays for some 50 meters through the shrubs. The hawk flew away without further attacks. Female XOO (incubating) was not involved.
8 December 1972	1	30	In border of secondary forest and wooded grassland, a hawk followed the flock (7 jays) at a short distance for more than 250 meters and attacked them at least twice. Jays attacked the hawk 5-6 times.
10 December 1972	1	10	In wooded grassland and edges of potato plot. Hawk attacked 4 times and was attacked twice by all 7 jays. Hawk flew away after chase following its fourth attack.
25 January 1973	1	7+	Two hawks attacked in open secondary forest at least three times. One hawk flew away after 2-3 minutes, the second one attacked once more. Again all seven jays in the flock chased the hawk and caused it to move to another tree.
12 April 1973	2	25–30 seconds	In dense pine plantation, two jays chased a hawk close to Nest 2. One of the jays was the male parent.
25 August 1973	3	35	In wooded grassland, a hawk attacked 10 times, three of the dives directed to the same banded immature (about 3 months old). See text for details on this instance.
2 September 1973	2	1–2+	I found all nine jays of this flock tightly clustered in the dense foliage of a cypress. A hawk came out of the same tree, circled twice above, and entered the cypress again, to be chased by the jays. Then the hawk flew away.
13 September 1973	2	3–4	In dense pine plantation, a hawk attacked banded adult jays twice. Jays clustered in two groups, of 6 and 3 respectively, low on the branches. Jays attacked the hawk twice, each time following a dive by the hawk. Hawk flew away at my approach. Jays gave the hawk-call several times during the episode.

The jays pecked at, and took, any prospective food items they found while foraging, usually on the same branch along which they were hopping, but not infrequently stretching up to take the item from the foliage directly overhead, or hanging down to reach the branch immediately below. While exploring the foliage at the tips of slender branches, the jays often hung upside down in titmouse fashion. They also sailed in pursuit of fleeing insects, and dropped to the ground to retrieve fallen items.

Hovering was also a rather common tactic in taking fruits and insects from the tips of small shrubs and ferns of the undergrowth. Sometimes they maneuvered quickly and snatched the food on the wing without visibly slowing down.

On the ground, Green Jays removed and turned over dry leaves and twigs by sweeping their bills sideways. Then they pursued and captured any fleeing prey, either by means of short flights, or by hopping after them. Dry, rolled-up leaves invariably held the attention of jays, which took them to a suitable perch nearby to peck them open, and extract whatever arthropods the leaves may have harbored.

Green Jays rarely ate the food immediately or at the site of capture. They usually carried the item to a convenient perch for further examination, to eventually peck it apart while held with the feet and swallow it in small bits. If disturbed, the jays flew off carrying the food in their bills, and resumed the procedure at another perch. The same treatment was given to all food items. The very small berries of *Palicourea* spp, only about five mm in diameter and with tiny seeds, were treated the same as big beetles, the hard exoskeletons of which the jays had to tear open. Occasionally, though, the jays swallowed relatively large insects entire. I saw a jay swallowing a katydid about 4 cm long, without first pulling off wings or legs.

In preparing hairy caterpillars, the jays beat them against a branch until the integument came off. In one of the stomachs analyzed, though, there was an entire saturnid caterpillar with highly urticant hairs (Alejandro Madrigal, pers. commun.).

While collecting food for nestlings or newly fledged young, Green Jays were likely to carry entire food items, usually crosswise in their bills, perhaps because the load of food already accumulated in the throat and mouth made difficult any dismembering by the usual hammering method. Besides, stopping to peck apart every prey would substantially increase the time needed to gather a mouthful of food. No further preparation of the food took place at the nest, and the items were fed entire to the young.

Table 3 gives the proportions of animal and plant materials found in four stomach samples.

The notion that Green Jays rob the eggs and young of other birds is widespread. Although I have no evidence of this predatory habit, neither from my observations nor from the analysis of stomach contents, the fact that jays often explored empty nests points to the possibility that they may prey on the contents of active nests.

Green Jays exploited several sources of food that became temporarily abundant. During a total of 10 hours and 35 minutes, from 9 May to 12 May 1973, I followed Flock 4 through a pine plantation that became affected by an outbreak of the defoliating caterpillars of *Glena bisulca,* a geometrid moth. Out of 72 instances of insects captured by the jays during that period, I was certain in at least 41 captures (69.5 percent) that the prey were larval and mature stages of the moth (15 larvae, 26 adults). The inchworms were

TABLE 3

Proportions of Plant and Animal Matter in Four Stomachs of Green Jays[1]

Type of food	*Specimens*			
	1	*2*	*3*	*4*
Insects	68.90	26.89	62.07	52.60
Vertebrates	----[2]	16.78	----	----
Seeds	31.30	33.67	37.93	17.20
Other plant material	----	22.65	----	30.20
Total animal matter	68.90	43.67	62.07	52.60
Total plant matter	31.30	56.33	37.93	47.40

[1] Percent of dry weight of the sample.

[2] Traces of lizard skin.

captured in the foliage near the tips of the branches, and the adults on the trunks. The Green Jays captured the adult moths either by simply picking them up, or by catching them on the wing as they fled.

The borders of recently plowed fields were very attractive to the jays, as they provided a variety of food items that would be unavailable if not uncovered by the plow. In such situations I saw Green Jays feeding on earthworms, grubs and nymphs of beetles, and crickets. On one occasion, the jays of Flock 1 were feeding on some white objects among the chunks of soil turned over by the plow the day before. After the jays left I examined the place and found four lizard eggs, one of which contained an embryo in an advanced stage of development. The jays had taken at least eight eggs, probably not all of them fertile, during the two or three minutes that they foraged there.

Green Jays were also regular visitors of corn plots. Their activities started as soon as the grain was ripe, but still tender. At that stage the jays opened the husks near the tip, and subsequently ripped them down to uncover more kernels. Even though the jays visited the corn plots almost daily, they concentrated on the few ears that had already been opened, either by themselves, or by squirrels *(Sciurus grantensis)*.

A variety of fruits also entered into the diet of the Green Jays. Among those taken most often were the fruits of *Solanum* spp, *Rubus* spp, *Miconia* spp, *Palicourea* spp, and *Clusia* ssp. All of these are trees and shrubs that grow profusely in the secondary forest, and produce small fruits less than 10 mm in diameter, except for *Clusia,* whose fruits are between 15 and 20 mm in diameter and open by themselves when ripe, exposing the reddish pulp that surrounds the seeds.

Breeding

I found seven active nests of Green Jays in my study area. I did not observe all seven nests throughout their cycles, as I found most of them at advanced stages of building, or already containing eggs or young. I was able to secure information of the duration of the several stages only for Nest 2 of Flock 2. Therefore, I extrapolated the data from this nest in reconstructing the breeding schedules of the other six (Figure 9).

There was a marked coincidence between the onset of breeding and the beginning of the rainy season during the first days of March 1973 (Figure 9). Flock 2, which had failed to raise a clutch of four beyond the nestling stage in November 1972, started to gather nest material on 2 March 1973, right after the first three rain showers. Flocks 1, 3, and 4 probably started nests between 16 and 25 March. I had no indications of breeding activity in these three flocks during the last months of 1972. Nest 1 of Flock 2 could have represented either a replacement clutch after a failure during the breeding season earlier in 1972, or a second clutch.

By the middle of May, two or three weeks before the peak of the rainy season, three of the flocks had young out of the nest. Flock 1A, which had started its first nest in close synchrony with Flocks 2 and 3 the third week of March, did not produce any fledglings until the middle of June, at about the peak of the rainy season. This delay was due to the failure of the two previous nests built by the flock since 25 March because of the splitting of the flock, which I described earlier.

Courtship

The existence of mated pairs in three of the flocks became evident at the end of February 1973. I had no evidences of more than one breeding pair in any of the four flocks of the study area.

These pairs often separated from the rest of the flock to forage by themselves, or just to perch together for periods of a few minutes, after which they went back to join the other jays. In all of eleven instances recorded, the female bobbed three or four times while perching close to the male, and the latter invariably responded by adopting the Sleek Posture, followed immediately on four occasions by Bill Caressing. Afterward, the female flew away from the flock, closely followed by the male. Their return to the other jays was always preceded by a new bout of bobbing by the female, and the male again followed her.

While foraging alone, the female frequently adopted the Courtship Begging posture after the male had captured an insect (five of seven times). Twice the male responded immediately by feeding the prey to the female; a third time he did so only after a short chase by the female; and on two occasions, the male eluded the female and ate the morsel himself. Perhaps the pair also selected the nest site during those short periods of isolation.

During the midday resting periods, both members of the pair perched together, frequently in bodily contact. Allo-preening invariably occurred on those occasions, sometimes with participation of a third individual. However, there were no instances of aggressive behavior by the prospective mates toward the third jay, and the latter was always allowed to preen the other two jays, or was preened in turn by one of them.

In general, while most instances of behavioral interactions between the mates took place while they were isolated, the proximity of any member of the flock never seemed to cause any disturbance to the pair, or to provoke aggression. The occurrence of all the behavior patterns referred to above extended well into the nest-building stage and alternated with the activities of this part of the breeding cycle.

Apparently, the pair-bond lasted for several breeding seasons. One pair (Female XOO and Male XBB) produced a clutch in November 1972 and another one four months later in March 1973, a dry season intervening during which there was no breeding activity.

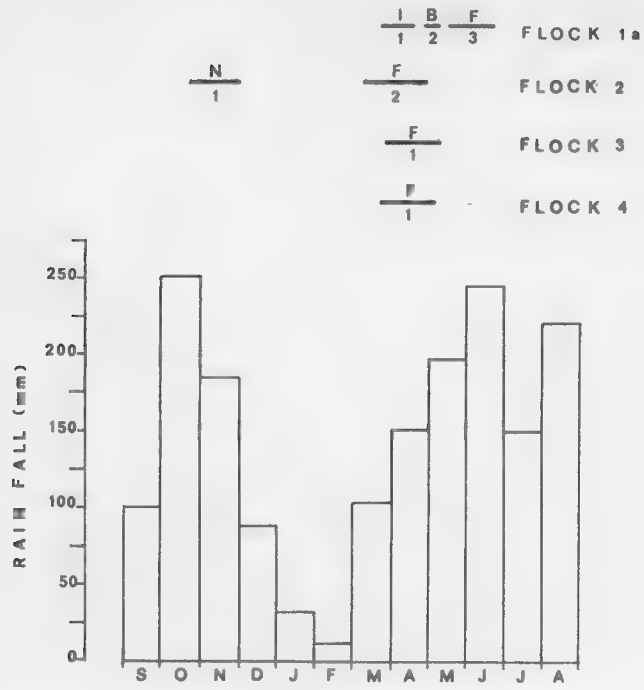


Figure 9. Breeding chronology of four flocks of Green Jays, and monthly rainfall at the study area from September 1972 to August 1973. Each horizontal bar represents the length of time during which that flock carried on activities at the nest referred to by the number below the bar. The letters represent the stage at which the activities terminated. N, nestling; I, incubation; B, nest-building; F, fledging.

The situation between Female XRM and Male Long Crest of Flock 1A was somewhat different. They had built three nests, the last one successful, during a period of three months (late March to mid June). About one week after the young fledged, Long Crest was seen courtship-feeding XMB, probably a female, of Flock 1A. Afterwards Long Crest moved to Flock 1B.

Nest-building

Both members of the mated pair accomplished most of the nest-building, with only occasional participation by other members of the flock.

For the second nest of Flock 1A, which I found perhaps two or three days after its initiation, Female XRM and Male Long Crest performed all the duties of carrying materials and building. However, in both cases, all members of the flock followed the building pair from the gathering places to the immediate neighborhood of the nest, sometimes singly but more often in pairs or threes.

Nest building activities were distributed into two daily periods, one between 07:00 and about 09:30, and the other between 16:00 and 17:30. The morning period started when one of the members of the pair, or both, gathered the first pieces of material in the same area in which the flock had been foraging, and carried them to the nest site, sometimes a distance of one-half kilometer. The rest of the flock followed and continued foraging at a short distance from the nest while the pair engaged in building. After this first trip, all the material was gathered from the neighborhood of the nest site.

The nest is a shallow, loosely woven basket of slender twigs, some of them as long as 25 to 30 cm. The inner cup contains rootlets, dry grass, pine needles, and other thin and flexible materials. The external diameter of one nest measured 23 cm, and the inner cup was 9 cm in depth. Even the material of the inner cup was so loosely arranged that sometimes the eggs could be seen from below the nest.

Green Jays usually build their nests on one or two lateral branches against the trunk of a tree. In one case, the nest (the third one of Flock 1A) was built in the fork of a slender branch, some 3.5 to 4.0 meters from the trunk. The two nests found in pines had been built to take advantage of the abnormal, forked growth of the trees, produced by an insect that destroys the terminal bud of the saplings, causing the branches of the knot immediately below to grow upward and form a strong, well protected receptacle.

I found Green Jays' nests in all types of vegetation, except for cypress and *Eucalyptus* forests. Table 4 summarizes the features of the location and habitat for six nests.

The nests were built in locations with various degrees of exposure. Nest 1 of Flock 2 was in a sapling surrounded by sparse shrubby vegetation that did not provide an overhead protective canopy, allowing the sun to fall directly on the nest during most of the day. This nest could be looked into from a trail on the hillside. Workers as well as cattle frequently used this trail, but jays did not seem very concerned. However, probably some kind of disturbance kept the brooding female away from the nest one afternoon, and the three nestlings died, perhaps due to exposure during the late evening.

The location of the first nest of Flock 1A was basically the same, and it was deserted after one of the four eggs in the clutch was broken by an ani.

Nest 3 of Flock 1A and Nest 2 of Flock 2 (Figures 10 and 11) were in more protected situations. The first one, with several overhanging branches, was in a patch of dense secondary forest with three well developed stories. The second nest of Flock 2, in a dense young plantation of *Pinus elliottii,* was equally well protected.

Nest 1 of Flock 4, also in a pine plantation, was more exposed, lower, and about five meters from the edge of a trail frequented by cattle, mule packs, and people. However, the jays managed to keep the nest undiscovered and undisturbed.

Egg-laying and Clutch Size

I could make no direct observations on the temporal pattern of egg laying. I gathered some data on this aspect only for the second nest of Flock 2. On 12 March, at about 09:35, Male XBB and Female XOO were seen carrying materials for the last time. On the morning of 14 March, when I finally found the nest, it contained two eggs. On 18 March, I found four eggs. Therefore, I assume that the nest was finished on 12 March, and that two eggs had been laid between 12 and 14 March. Two more were deposited between 14 and 18 March. It seems reasonable, then, to assume that Green Jays lay their eggs at 24-hour intervals, and that the clutch had already been incubated for at least one day when I found the nest. In the Tufted Jay, the interval between consecutive eggs is also 24 hours (Crossin, 1967).

For three nests, the clutch size was four. These nests were the first of Flock 1A, and the first and second ones of Flock 2. Three young fledged from Nest 1 of Flock 4; and Flock 3 was seen feeding four young that had fledged about two weeks before. Three young fledged from Nest 3 of Flock 1A, but I could not determine whether there was a fourth egg, infertile, as was the case with the first clutch of Flock 2.

A Mexican Green Jay in captivity laid a clutch of four eggs (Roles, 1971).

Rowley (1966) reported on a nest of Green Jays with four fresh eggs in the Sierra Madre Del Sur, Oaxaca, Mexico.

The eggs are sparsely to densely blotched with brownish spots on a bluish white background. Seven eggs averaged 29.9 mm in length (range 28.4 to 31.0 mm), and 22.1 mm in breadth (range 21.5 to 22.5 mm). Their average weight was 7.7 grams (range 7.1 to 8.1 grams).

Incubation

I was able to study two nests during at least a part of their incubation periods. Both were nests of the same pair (XOO and XBB) of Flock 2. The female spent all of her time at the nest sitting tightly, moving only momentarily to roll the eggs. Only those disturbances that involved the nest tree, or the nest itself, caused her to leave. That was the case when Giant Cowbirds came to perch a few feet from the nest, and also on two occasions when I climbed the tree to check the nest. At one of the nests, the contents of which I checked daily by means of a mirror, the female always waited until the mirror was directly above her before she flew away.

Early in May 1973, I had the opportunity to watch the activities of a female (XRM) during her inattentive periods. When leaving the nest, she remained only a few seconds in the neighborhood to stretch her limbs and preen. Then she went either directly to the area of activity of the flock, whenever their calls could be heard, or to a succession of vantage points from which she delivered a series of long distance contact calls, until the other members of the flock responded. The female joined and followed the flock for up to one hour.

Sometimes, usually at the end of long attentive periods, the female left the nest and followed the male immediately after he had fed her at the nest. Several times, also, I saw the female coming back to the nest escorted by the male, who then fed her at the nest. Other jays occasionally joined the male in escorting the female.

TABLE 4
Vegetation Features of Six Green Jays' Nest Sites

Nest	*Height of nest (m)*	*Height of nest tree (m)*	*Tree Species*	*Vegetation type*
Flock 1				
Nest 1	5.0	5.8	*Vismia* sp.	Secondary forest-grassland edge
Nest 2	7.0	8.5	*Vismia* sp.	Two-story secondary forest
Nest 3	10.0	10.5	*Myrcia* sp.	Three-story secondary forest
Flock 2				
Nest 1	4.0	4.5	*Alchornea* sp.	Savanna
Nest 2	8.0	9.5	*Pinus elliottii*	Pine plantation
Flock 4				
Nest 1	4.5	5.5	*Pinus patula*	Pine plantation

Figure 10. Site of Nest 2 of Flock 2 in a pine plantation.

While foraging along with the flock, the female frequently begged from the male, who responded by feeding her any items he had gathered. Sometimes, though, the female did not wait to be fed on the spot; while close to her mate, she bobbed several times and flew back to the nest, closely followed by the male. This ended the inattentive period, and the male returned alone to the foraging area.

The female (XOO) at Nest 1 was fed only six times in 31 hours of observation. Her periods off the nest averaged 37 minutes (n = 9, range 16 to 80 minutes), and she spent 18 percent of the observation time off the nest. At Nest 2, she was fed 26 times in 54 hours of observation, and her inattentive periods averaged 26 minutes (n = 18, range 2 to 81 minutes). She spent 15 percent of the observation time off the nest. The increased time at the nest, and the reduction in the average inattentive period at the second nest, probably reflect the increased frequency of feeding visits by the male and other members of the flock, consequently reducing her need to leave the nest and feed by herself. The incubation rhythms for this female at her two nests are detailed in Table 5.

The male provided the bulk of the food to the incubating female. I recorded feeding visits by other jays only during the last three days of the incubation period at the second nest of Flock 2. In such instances, the visitors did not feed the female with the same readiness as the male. Even though the jays came to the nest with full throats, they stood hesitantly at the border of the nest while the female begged. At least once, the visitor flew away without giving the food to the female.

Even at the first nest, however, all the members of the flock (five in addition to the mated pair) came individually to the nest, whether the female was there or not, and examined the nest for a few seconds. The female did not seem to be bothered by the visitors, and exchanged soft *rak* calls with them. Once, an immature (XMM) came to the nest and crossed bills gently with the female. Another immature (RRR) looked at the nest along both sides of the sitting female as if trying to see the interior. Three more jays took away dry leaves that had fallen in the nest. All these inspection visits occurred within the last two days of the incubation period.

Only the female incubated. However, on 12 November, at Nest 1, an unbanded immature ("Amarillo") came to sit on the eggs at 13:28. The female (XOO) came three minutes later and shoved aside the other jay to sit on the eggs. Amarillo stood at the rim of the nest for half a minute more, then flew off.

Both during the incubation and nestling periods, the jays were very silent around the nests. The only vocalizations normally given were the soft *rak* and the *choonk* that the visitors exchanged frequently among themselves and with the incubating female while approaching the nest with food. Green Jays chased away birds of other species quietly, but any individuals around the nest gave alarm calls at my approach to the nest. The female, though, always remained silent at these times.

Females approached the nest in a rather direct way, without stopping for any length of time in the neighborhood. Males were more cautious while carrying food to the nest, either for the female or the young.

Based on my assumption that the last egg of the clutch in the second nest of Flock 2 was laid on 16 March, and that the female started to incubate at that

Figure 11. Site of Nest 2 of Flock 1A in secondary forest.

time, the length of the incubation period for the Green Jay is about 17 days. I could make no direct observations on the chronology of hatching for this nest, as it was inaccessible for daily checking. However, on the morning of 2 April, the female swallowed egg shells at 07:50, 10:34, and 10:39, thereby terminating the incubation period.

Roles (1971) also figured the length of the incubation period as 17 days. His captive female apparently started to incubate after she had laid the third of four eggs. The first young of this clutch hatched 15 days after the last egg had been laid, and the other three young one day later.

In the Tufted Jay (Crossin, 1967) incubation starts after the second or third egg has been laid, and this also may be the case with the Green Jay. In the first nest of Flock 2, two young hatched late in the afternoon of 20 November or early in the morning of the following day. A third egg hatched before 08:00 on 22 November, at least 24 hours later than the first two, which indicates that incubation may start before the clutch is completed. If this is true, the incubation period for the Green Jay would be at least 18 days.

TABLE 5

Attentiveness by a Female[1] at Two Nests During the Incubation Period

Days before hatching	*Observation period (hours:minutes)*	*On nest (minutes)*	*Off nest (minutes)*	*Percentage of observation time on the nest*
Nest 1[2]				
9	9:00-14:00	***215, 29***[3]	56	81.3
8	7:05-12:05	***159, 111***	30	90.0
6	8:45-13:45	***118, 159***	23	92.3
5	8:10-12:10	***92,*** 100, ***4***	16, 28	81.0
3	11:05-15:05	***35,*** 125	80	66.0
2	9:15-13:15	***95,*** 87, ***11***	18, 29	80.0
1	7:00-11:00	***91, 93***	56	76.0
Nest 2[4]				
14	7:15-12:15	***278***	**22**[5]	92.7
13	12:30-17:30	***155, 118***	27	91.0
12	6:30-11:30	135, ***54***	**30**, 81	63.0
11	11:25-15:25	***45,*** 119, 30	21, 25	80.8
8	13:00-18:00	***197, 65***	38	87.3
7	9:00-14:00	***109,*** 139	27, **25**	82.7
6	10:45-15:45	***191, 66***	43	85.6
5	13:00-18:00	***147,*** 89, 30	23, 11	88.6
3	6:30-11:30	214, ***45***	**19**, 22	86.3
2	13:00-18:00	***142,*** 8, 93, 15	30, 2, 10	86.0
1	11:00-16:00	***83, 210***	7	97.7

[1] Banded Female XOO.

[2] Observed from 12 to 20 November for a total of 31 hours.

[3] Bold-faced numbers indicate that the female was on the nest when the observation period began or ended.

[4] Observed from 19 March to 1 April for a total of 54 hours.

[5] Bold-faced numbers indicate that the female was off the nest when the observation period began or ended.

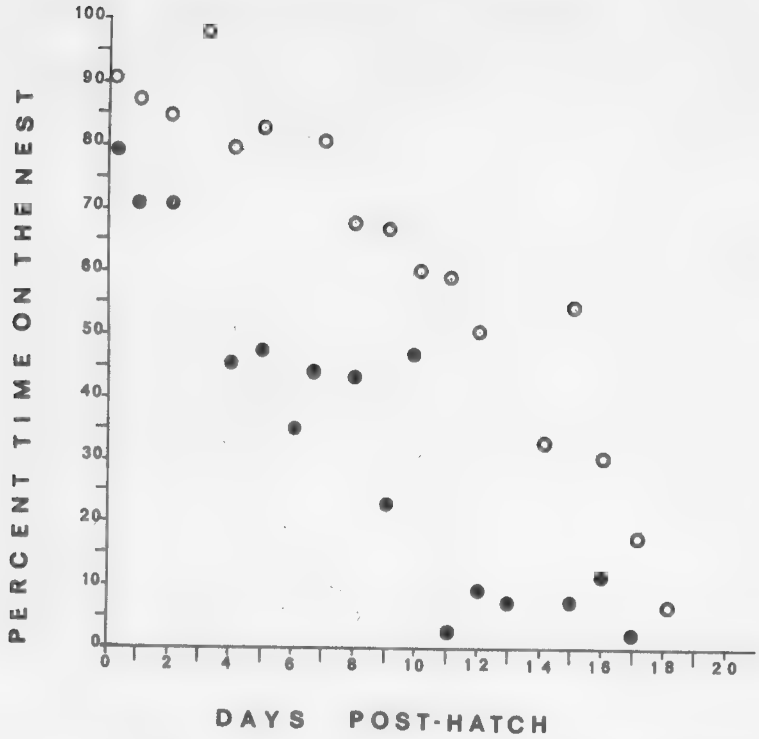


Figure 12. Percentage of time spent on the nest by two females during the nestling period. Clear circles, Female XOO at Nest 2 (Flock 2); black circles, Female XRM at Nest 3 (Flock 1A).

Brooding

During the final days of incubation and the first five days after hatching, one female (XOO) spent about the same proportion of the observation time at each of her two nests. At her second nest, as she started to participate more actively in feeding the young, her attentiveness decreased steadily, and her periods off the nest became more frequent and lasted longer. Figure 12 summarizes my observations on attentiveness at three nests, two of them up to fledging.

Until the fifth or sixth day of the nestling period, the female brooded the young almost as tightly as she had covered the eggs. During the midday hours on sunny days, she sat more loosely, with open wings resting on the rim of the nest. Later on in the nestling period, the female fully covered the young only during rain showers, or under strong wind. Otherwise she covered only half of the nest.

From the fifteenth day on, the increased mobility and activity of the nestlings made the female's attempts to cover them awkward, and she was able to accomplish it properly only when the young crouched low in the nest. At about this age the young of both nests started to respond with greater strength in their movements to the arrival of adults with food, rising abruptly from the bottom of the nest, and literally lifting the female with their heads.

This female (XOO) ceased to cover the young altogether during the day three days before they fledged. Another female (XRM) brooded her young a small proportion (up to 12.3 percent) of the time under observation during the last seven days before fledging, apparently forced to do so by the intense rain showers and the almost constant wind that threatened to blow the nestlings from the nest.

Only the female parent brooded the young, except for a few short and incomplete attempts at covering the nestlings by both the male and two helpers. In such instances those individuals never went beyond half-sitting for a few seconds, after which they went back to perch on the rim of the nest.

TABLE 6

Time Contributed to Nest Guarding[1] by Jays Other Than the Female Parent

	Nest 1 *Flock 2*	*Nest 2* *Flock 2*	*Nest 3* *Flock 1A*
Flock Size	8	5	3
Observation time during the nestling period (hours:minutes)	27:00[2]	98:30	88:45
Percentage of time nest was unattended during observation periods	(21.6)[3]	(36.4)	(64.2)
Female's inattentive time	8:49 (100.0)	44:48 (100.0)	58:08 (100.0)
Male parent on guard		1:50 (4.1)	0:12 (0.3)
Helpers on guard			
"Amarillo"	2:56 (33.3)	5:47 (12.9)	
RRR		1:35 (3.5)	
XMM		0:15 (0.5)	
XYM			0:53 (1.5)
Time nest guarded	2:56 (33.3)	9:27 (21.0)	1:05 (1.8)
Overlap of guards and female parent	0:00	0:45 (1.6)	0:00
Number of inattentive periods by female	8 (100.0)	64 (100.0)	56 (100.0)
Number of guarding periods by males and helpers during the female's inattentive periods	6 (75.0)	47 (73.5)	11 (19.6)
Number of inattentive periods fully covered by guards (percent)	0	11 (17.2)	0

[1] I did not count as "guarding" the time spent in feeding visits, unless the visitor remained at the nest for at least one additional minute after the young were fed.

[2] All numbers with a colon indicate hours and minutes.

[3] All numbers in parentheses are percentages.

However, jays other than the female parent often came to stay at the nest for variable periods of time, on occasion for over one hour. During those periods, the "guards" engaged in long sessions of nest cleaning. The guards also begged for food from any other member of the flock that arrived at the nest.

Sometimes it was necessary for the female returning to the nest to brood to shove off the guard.

At two of the nests (Table 6), the time contributed by the male and the several helpers made up for an appreciable proportion of inattentiveness by the female. In only one nest was there a small time overlap during which the female and another jay guarded the nest simultaneously; most of the guarding took place when the female was off the nest. Only one out of 64 guarding periods recorded entirely overlapped with the female.

When guarding the nest, all jays showed the same reluctance as the female to leave when alarmed. For every member of Flock 2, I recorded at least one instance in which a guarding jay remained at its post in spite of the proximity of aggressive interactions between other members of the flock and intruders of other species, mainly Giant Cowbirds.

At both nests of Flock 2, Amarillo contributed the longest (up to 1 hour and 11 minutes) and most frequent guarding visits. Of 11 guarding periods that covered completely the absence of the female, Amarillo performed eight, the male parent (XBB) two, and one period was shared by XBB and RRR. The latter helper and XMM started to guard only at the second nest.

Feeding of the Nestlings

The role of the females for the first days of the nestling period was restricted to brooding the young. Upon the arrival of the male or any other jay at the nest, the female assumed the courtship begging posture, while still covering the young. After receiving food, she uncovered the nest, allowing the visitor to feed the nestlings. The female then proceeded to feed them herself with whatever food she had obtained, frequently taking items from the mouth of one young jay and transferring them to another nestling's gape as if redistributing the food.

From the beginning of the nestling period, the female had to obtain her food by herself, and although she still followed the flock during her periods off the nest, I never saw the female beg from the male when out of the nest. Only within the first four days after the eggs hatched did the females occasionally swallow the food brought by the visitors. However, since the feeding of the female by another jay was immediately followed by her redistribution of the food among the young, I could not be sure in most instances whether the female had swallowed her share or was actually passing all of it to the young.

Helpers at the nest were common for at least three of the flocks in the study area (Figure 13). For Nest 2 of Flock 2, and Nest 3 of Flock 1A, I secured data on the relative contributions to the feeding of the young throughout most of the nestling period (Tables 7 and 8). Only Long Crest of Flock 1A and Amarillo of Flock 2 were unbanded.

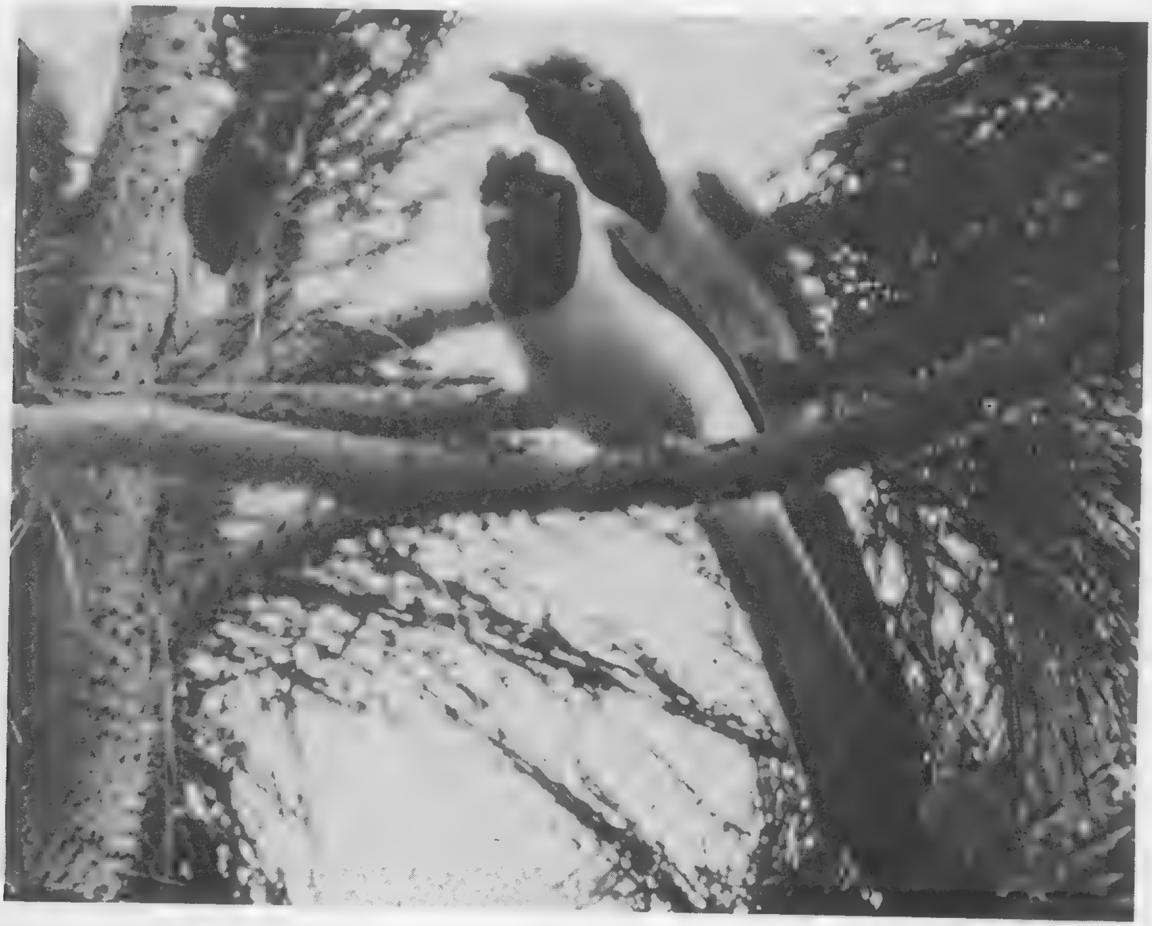


Figure 13. Male parent (XBB) and a helper ("Amarillo") of Flock 2 about to feed the nestlings at Nest 2.

TABLE 7

Contributions by Members of Flock 2 to the Feeding of the Young at Nest 2, and Feeding Rates, 2 to 23 April

Days after hatching	*Observation time (hours:minutes)*	*Number of visits by jays in Flock 2*						*Total visits*	*Visits per hour*
		XOO	*XBB*	*RRR*	*XMM*	*"Am"*	*Un-identified*		
0	5:30	—	6	8	1	—	1	16	2.9
1	5:00	—	7	5	3	1	2	18	3.6
2	5:00	—	7	5	3	4	—	19	3.8
3	5:00	1	10	6	3	3	—	23	4.6
4	5:00	—	7	7	2	4	—	20	4.0
5	4:30	—	6	4	2	2	1	15	3.3
7	5:30	—	11	7	6	2	—	26	4.7
8	4:00	2	6	4	2	2	—	16	4.0
9	5:30	1	11	5	4	5	—	26	4.7
10	6:00	2	16	9	12	4	1	44	7.3
11	6:00	—	12	7	—	5	—	24	4.0
12	6:00	4	13	5	3	5	—	30	5.0
14	5:00	3	10	8	—	1	—	22	4.4
15	5:00	3	13	5	—	4	—	25	5.0
16	5:00	3	8	4	1	6	—	22	4.4
17	4:00	4	6	4	1	4	—	19	4.7
18	5:30	7	7	6	3	3	—	26	4.7
19	5:00	5	10	5	—	5	—	25	5.0
21	6:00	11	16	9	4	10	—	50	8.3
Total	98:30	46	182	113	50	70	5	466	
Percentage		9.8	39.1	24.2	10.7	15.0	1.1	100	

Besides the parents (XOO and XBB) of Flock 2, five other jays fed the young at Nest 1. The male and female had been banded during the incubation period, and three of the helpers were banded during the first week of the nestling period. Four of the helpers at this nest had nuchal bands in various degrees of definition, from faint to well marked. A fifth one had almost pure white crown and nape, and a well developed fronto-nasal tuft, comparable only to that of the mated male (XBB). At Nest 2, four months later, the nuchal markings had entirely disappeared in all three remaining helpers, and their crowns and napes were as white as those of the mated pair.

I was able to study Nest 1 of Flock 4 during only four hours on the same day I found it, as the three nestlings fledged prematurely. At one time all four attendants, the mated pair and two helpers, gathered at the nest to feed the young. It seems, therefore, that all the jays that belong to a flock participate in feeding the young.

There were individual differences, both in frequency of feeding visits, and in regularity (Table 7 and Figure 14). At Nest 2 of Flock 2, the presumed male (XBB) regularly contributed more visits than the female and any of the helpers. At Nest 3 of Flock 1A, the only helper contributed even more feeding visits than the male of that nest.

The contribution of two female parents (XOO and XRM) at their nests were smaller than those of any other jays of their respective flocks. At Nest 2, I recorded the female (XOO) feeding the nestlings for the first time on the fourth day after hatching, after 15.5 hours of observation during the three previous days. She did not feed the young during the following three observation sessions (15 hours), resumed regular participation on my eighth session, and failed once again on the eleventh one.

I did not record any feeding visits by the female of Flock 1A (XRM) during the first three observation periods (16 hours); but once she started, her contribution surpassed that of the most active helper (RRR) of any flock.

Although I had no way to evaluate the actual amount of food delivered at each feeding visit, it was clear to me that the mated males were bringing more food per visit than the helpers and the females. Both males (XBB and Long Crest) were the ones that brought to their respective nests the largest prey, mainly lizards and katydids. Also, their throats were always fully distended, and they sometimes carried additional items in the semi-open bills, while the helpers and the females only occasionally gave me the impression of bringing such big loads.

Figure 15 shows the distribution of hourly feeding rates throughout the day (12 hours) for two nests. The hourly rates were obtained by adding the average rates of the corresponding half-hour periods. At Nest 2 of Flock 2, the feeding effort appeared unevenly distributed, with three major peaks and with intervening periods of relatively lower activity. At Nest 3 of Flock 1A, though, the graph suggests a more sustained effort throughout the day, with less defined peaks of feeding activity.

The overall hourly feeding rates were 4.73 (1.18 per young) at Nest 2 of Flock 2, and 3.85 (1.28 per young) at Nest 3 of Flock 1A. At the former, the feeding rates fluctuated between three and five per hour during the initial six days of the nestling period. Later on, the fluctuation narrowed to between four and five feeding visits per hour, and steadily approached the upper limit of five. On the last day of the nestling period, the young received a sudden increase to more than eight feedings per hour, produced by an increase in the activity of all five attendants. The peak on the tenth day was brought about mainly by an unusually intense participation by XMM during that session (Figure 16).

At Nest 3 of Flock 1A, the hourly feeding rates increased smoothly from two to almost six during the first 14 days post-hatching (Figure 16). Both the reduction and the wide fluctuation of the feeding rates recorded during the last three days of the nestling period were probably caused by the strong winds and rain showers that occurred on those days.

Both parents and helpers shared the duties of nest sanitation, consisting mainly in carrying away the fecal sacs produced by the young after they were fed. Therefore, at any given visit, an attendant performed two functions—feeding the young and removing the fecal sacs. Green Jays swallowed the fecal sacs produced by the young during the first seven days after hatching. Afterward, the attendants carried the sacs away hanging from the tips of their bills, and sometimes in their throats, to drop them some distance from the nest.

After the seventeenth day post-hatching, the young defecated sometimes on the rim of the nest. These sacs were picked up by the first jay that came to feed the young. In four old nests of Green Jays I found only traces of fecal matter, mostly on the outside of the nest.

Besides fecal sacs, the attendants took away dry leaves and twigs that had fallen onto the nest.

Interactions at the Nest

Often as many as four jays, all bringing food to the young, were at the nest at the same time. Seemingly, though, these frequent concentrations did not release any overt agonistic behavior in the jays.

At the beginning of the nestling period, any jay bringing food to the young gave part of it to the brooding female or to any other jay that happened to be guarding the young, and then both birds fed the young. I did not record any instances of a jay other than the female swallowing food brought by another visitor.

Although any jay initially transferred part of the food readily to any other jay that begged for it at the nest, the willingness of the visitors to give food to guarding jays declined abruptly about the third day of the nestling period, with the exception of the male parent. The intensity of begging by the guards, however, did not decrease correspondingly, thus causing the only apparent social tension I recorded at the nests. Frequently the guarding jay attempted to snatch some food, and then both tugged at a morsel until one of them succeeded in snatching it from the other and quickly fed the item to the nestlings. This interaction delayed feeding by no more than 30 seconds.

The male parent responded to other jays begging at the nest with the same readiness as he did with the female. The latter, on the contrary, never gave any food to jays other than the nestlings.

I recorded quarrels of the type described above in every observation session between the third and the fifteenth days post-hatch. From this day on, the frequency of interactions decreased as both the parents and the helpers devoted less time to guarding the nest.

Post-fledging Care

Immediately upon leaving the nest, the fledglings took cover in dense shrubby vegetation, where the attendants continued to feed them. It was impossible for me to secure detailed information on feeding rates and relative contributions by the members of the flock, due to both the character of the vegetation and the increased excitability of the adult jays during this particular phase. All attempts I made to approach the area of the recently fledged birds resulted in intense scolding by the flocks.

Sometimes coming within two meters of my post, every member of the flock participated in the scolding, constantly giving alarm calls, and occasionally uttering rage calls as they dive-bombed whenever I closely approached the spot where the juveniles hid. In no instance, though, did the jays make contact in their attacks. They were far more timid than Blue Jays, which do not hesitate in pecking at potential predators while defending nests and young.

At least two or three Green Jays were present in the mobbing assembly at any moment; but they were not always the same individuals. After having scolded for a while, one or two jays slipped away quietly for several minutes to feed the young. This relay defense system probably enabled the jays to stay aware of the position of a predator, and to harass and distract it without upsetting the feeding of the young. At the same time, their constant and loud calling close to the intruder was highly effective in screening any begging calls and gurgling noises by the juveniles that could betray the latter's location.

The parents of Flock 2 participated much less in mobbing than the helpers. I saw both of them several times going away from the scolding assembly, and shortly afterwards, flying with full throats into the general area of the fledglings.

This defensive strategy was repeated in all four flocks that I observed under similar circumstances. Even though Flock 1A engaged in the same behavior in protecting the young fledged from Nest 3, I succeeded in capturing and banding all three fledglings, the first one right after it came down the nest tree.

In 11 instances of feeding the young at Nest 3 of Flock 1A recorded from 23 June to 9 July, one was by male Long Crest, three by a female (XRM), and seven by the only helper (XYM). However, these numbers may not represent their actual relative contribution; for later the female parent (XRM) devoted all her time to scolding me whenever I got close enough to make observations. After the first week post-fledging, the helper (XYM) ceased to participate in mobbing almost completely, and usually foraged quietly, always closely followed by the juvenile.

Long Crest deserted this flock about 24 June, and the helper (XYM) and the female (XRM) then undertook the care of the young, of which only one (XYR) survived beyond 28 June. By 1 July, another jay (XYB) transferred to Flock 1A, but I never saw this jay carrying food or feeding the young, and it was more timid in its scolding than the other members of the flock.

I did not record any feeding instances beyond 9 July. However, the surviving young (XYR) kept begging for food from the helper (XYM) until as late as 29 August without getting any response. By 10 September, the young jay and the helper still kept consistently within a short distance of each other, and constantly exchanged contact calls. Although the female parent and the new flock member foraged together all the time, neither of them showed the same concern for the juvenile as the helper (XYM).

Behavior and Development of the Young

Green Jays hatch naked and blind. During the first eight days after hatching, the young restricted their activities to begging from the attending jays that came to the nest, and often in the absence of attendants. Wing- and neck-stretching became frequent movements from the sixth day on. At the end of the first week after hatching, emerging feather sheaths outlined well-defined tracts of feathers.

From the twelfth day on, the young gaped in response to the soft calls given by attending jays when approaching the nest. However, the begging response

TABLE 8

Feeding Rates and Contributions by Members of Flock 1A to the Feeding of the Young at Nest 3, 1 to 18 June

		Number of visits by jays of Flock 1A					
Days after hatching	*Observation period*[1]	*XRM*	*"Long Crest"*	*XYM*	*Uniden-tified*	*Total visits*	*Visits per hour*
1	6:00	—	6	8	—	14	2.3
2	4:00	—	3	5	—	8	2.0
3	6:00	—	7	7	—	14	2.3
5	6:00	2	7	11	—	20	3.3
6	6:00	1	8	9	1	19	3.1
7	6:00	5	10	9	—	24	4.0
8	6:00	3	12	8	—	23	3.8
9	6:00	7	7	8	—	22	3.6
10	6:00	6	9	9	1	25	4.1
11	5:00	5	7	7	—	19	3.8
12	6:00	9	8	9	3	29	4.8
13	6:00	13	9	13	—	35	5.8
14	5:00	11	7	10	—	28	5.6
16	3:45	7	3	2	—	12	3.2
17	5:00	9	7	7	3	26	5.2
18	6:00	8	8	5	3	24	4.0
Total	88:45	86	118	127	11	342	
Percentage		25.2	34.5	37.1	3.2	100	

[1] Elapsed time in hours and minutes.

was still oriented upwards, even though the visitors approached from the side. At this age the young raised their rumps and rapidly shook their tails sideways before defecating. Whenever an attendant was at the nest, it responded to these movements of the young by taking the fecal sac directly from the cloacal aperture.

At fifteen days of age, the nestlings became more active, frequently perching on the rim of the nest for several minutes, either to rest, exercise their wings, or stretch their limbs. Preening also became a major activity, and the primaries, by then more than half out of their sheaths, received most of the attention.

Seventeen-day-old jays at one nest fluttered to the ground but were unable to fly. While being handled, they produced rage calls identical to those given by grown jays in similar situations.

From the eighteenth day on, the young left the nest for short periods and moved slowly for a few inches along the lateral branches. These excursions did not last more than one minute, after which the young went back to the nest. All the young at a nest started this new activity within the same day.

The three young of the third nest of Flock 1A left the nest on their own at nineteen days of age. At 06:53, two of them came out of the nest and started to climb down the nest tree, moving cautiously along the branches. The third one followed 15 minutes later. At 09:00, one of the first two came down to a shrub directly below the nest, no more than three meters high.

At the second nest of Flock 2, the young did not fledge until early in the morning on their twenty-second day.

A brood of Mexican Green Jays in captivity left the nest "at nineteen days old . . ., prematurely it seemed, as not one could fly" (Roles, 1971).

At fledging, the power of flight of the juveniles was very limited, although they might fly for short distances. Their directional control was nil, and they were unable to avoid obstacles. However, the juveniles rarely resorted to flight, and most of their locomotion was restricted to hopping along branches.

During the first seven days after fledging, the juveniles remained in dense shrub vegetation where they continued to be fed by both their parents and the helpers. As they drifted through the shrubbery, covering sometimes as much as 150 meters in a day, the young kept in contact with each other, and with the attendants, by means of constant *rak* calls. Their vocal activity ceased altogether as soon as one of the attendants called in alarm.

At 14 days post-fledging, the juveniles could be seen in more open vegetation near the borders of secondary forest patches. Still, they were noticeably less active than the other jays, but they could fly with much better control than before. One juvenile of this age performed several gliding flights, perhaps after flying insects.

As the juveniles gained skill in their movements, they started following the flocks and, except for the young's begging, their behavior became similar in all aspects to that of the older jays. At 21 days post-fledging, a juvenile (XYR) participated for the first time in scolding me along with other members of its flock.

Even though juveniles continued to beg from any other jays that came close, they got very little food from their flock companions. On the other hand, at day 25 after fledging, the young jays were already proficient in capturing by themselves a good share of the food, and very frequently they ate the small fruits of *Miconia* and *Palicourea.* Forty days after fledging, the skill of the juveniles in capturing insects was comparable to that of older jays.

When the young of the second nest of Flock 2 were more than three months old, I recorded one instance of begging from the female. The female did not respond, but the young followed her and begged for about 50 meters before giving up.

At the end of the study period in October 1973, all the young still remained with their parental flocks, even though they were fully independent of older birds for feeding.

Discussion: Advantages of Flocking and Helpers

The occurrence of flocks of fixed composition the year around, and the contribution by individuals other than the parents in feeding and protecting the young, are the most relevant features of the Green Jay's social system. Many other species of neotropical jays have developed a similar system of cooperative breeding. Brown (1974) provided a general review of the known social systems in this particular group of birds, and presented a theory on the evolution of communal breeding. This discussion concerns mainly the adaptiveness of the social characteristics of the Green Jay.

During the non-breeding season, defense from predators is the major aspect in which Green Jays benefit from their gregariousness. Their anti-predator defense system, which includes the detection of potential predators, the spreading of the alarm by means of special calls, and the harassment of predators derives efficiency from the active participation of all the members of the flock and from their concerted action. Perhaps it is significant that birds of prey such as Roadside Hawks and Broad-winged Hawks, which seemingly do not represent any actual danger for the jays, were often attacked and scolded by single individuals.

Foraging in flocks does not seem to confer on the Green Jays any particular

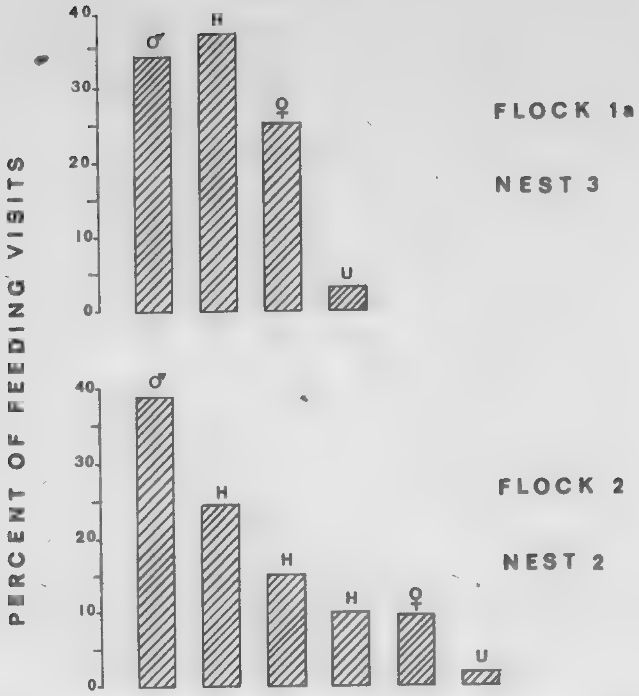
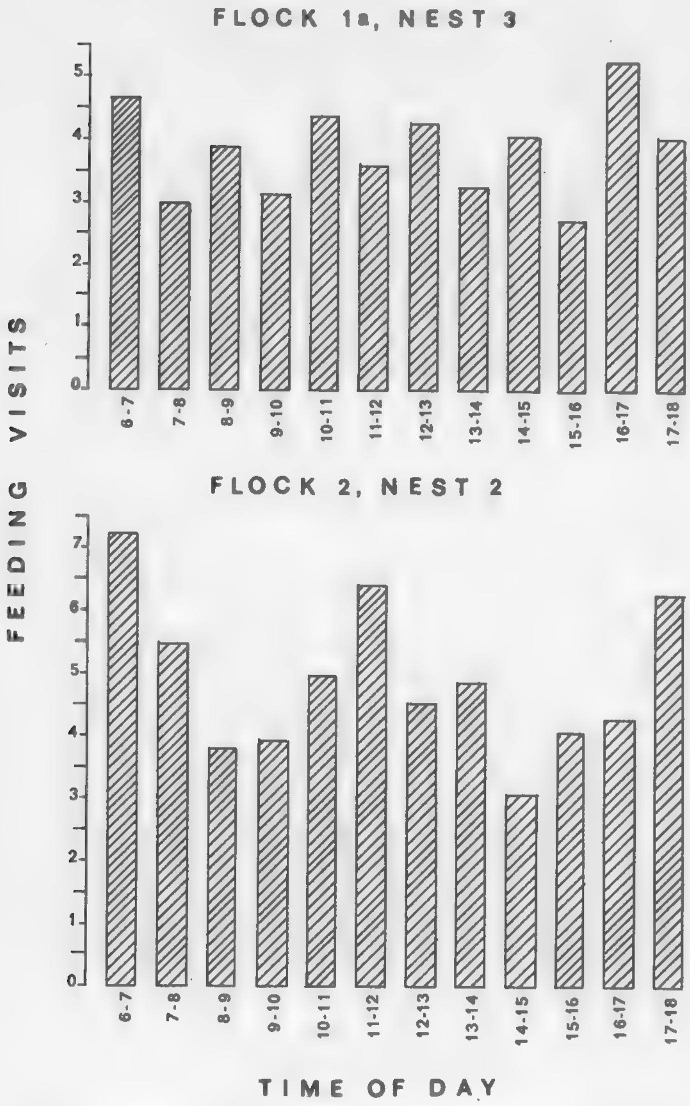


Figure 14. Relative contributions by members of two flocks to the feeding of the nestlings.

advantage in their feeding efficiency, since their usual feeding maneuvers, and the distance kept between individuals while searching for food, are not consistently conducive to the type of cooperative feeding in which the activity of an individual facilitates the capture of prey by another—for example, by flushing insects. Nevertheless, considering that Green Jays keep in sight of each other most of the time, it is likely that they may benefit from the discovery of certain localized and abundant sources of food by any one of the members of the flock. This was the case, for example, in pines heavily infested with defoliating caterpillars. Also, the utilization of these concentrated resources is facilitated by the reduced intra-flock aggression. The habit of the jays of taking food items away from the place of acquisition to peck them apart, therefore leaving the place free for another jay, is responsible in part for the absence of aggressive interactions and for the efficient sharing of the food.

By keeping aware of the locations of the other jays in the flock while foraging, they probably avoid wasting time in searching places already emptied of food. Balda *et al.* (1972) suggested that the efficient predator-warning system of Piñon Jay flocks allowed the birds of other species, temporarily associated with the jays, to forage more efficiently by concentrating more in their feeding activities. In the Green Jays, the sentry habit is not so well developed as in the Piñon Jays, but the former certainly make use of the alarm calls given by the first individual that detects an intruder.

The prolongation of gregarious habits into the breeding season conferred to the Green Jays additional advantages related to breeding success. Besides the mated pair, all the other members of a flock had a part in feeding the young, in nest sanitation, and in the defense of nestlings and juveniles. In one of the nests (the third one of Flock 1A), the contribution by the only helper amounted to more than 37 percent of the total number of feeding visits (Figure 14). Although the sample size is very small, a comparison between flocks shows a trend in the relationship between the number of helpers and the breeding success, here expressed as the percentage of the young that survived to the end of the study period, or three and one-half to five months after fledging (Table 9). I did not


FLOCK 1a, NEST 3

FLOCK 2, NEST 2

Figure 15. Variation of hourly feeding rates throughout the day at two Green Jays' nests.

include in Table 9 Nest 1 of Flock 2 because its failure could have been produced by the mist-netting and banding of the associated jays. I also excluded from the table Nest 1 of Flock 1A, the eggs of which were abandoned due to predation shortly after they were laid, and Nest 2 of the same flock, in which no eggs were laid.

There are several ways in which the number of helpers could affect the survival of the young. In the first place, as all the members of the flock feed the young, those nests with fewer helpers should experience a reduction in the feeding rates, and consequently, in the amount of food supplied to the young in those nests. Actually, though, in the nest with only one helper (Nest 3 of Flock 1A) the hourly feeding rate per nestlings was higher (1.28 visits per nestling) than at Nest 2 of Flock 2 (1.18 visits per nestling) attended by three helpers. The clutch at the first nest was only three eggs, but probably even with a full clutch of four, the smaller flock (1A) could have raised the young to the fledgling stage with an additional effort by the female (Figure 14) and under similar conditions of food availability. Still, it is likely that flocks with more helpers are more successful in raising young under conditions of food scarcity.

On the other hand, the helpers also contributed to breeding success by protecting the nestlings during inattentive periods of the female parent. At nests attended by a larger number of helpers (Nest 2 of Flock 2, Table 6), the latter guarded the nest for a larger percentage of the female's inattentive time than at nests attended by fewer helpers (Nest 3 of Flock 1A). That is, larger flocks were able to devote more time guarding the nest than smaller ones.

The number of helpers also affected the contribution of the female parents in feeding the nestlings and, as a result, the time that the female spent brooding. Female XOO, aided by three helpers at Nest 2 of Flock 2, contributed only 9.9 percent of the feeding visits, and spent 45.5 percent of my observation time off the nest. At Nest 3 of Flock 1A, with one helper, female XRM contributed 25.2 percent of the feeding visits, and was off the nest 65.5 percent of the observation time, thus reflecting the additional effort made by the female in order to make up for fewer helpers (Figure 14, Tables 7, 8, and 9).

Unfortunately, the feeding rates after fledging remain unknown, but my observations indicate that the young are fully dependent on the parents and their helpers for at least 20 days after fledging, and that the increased mobility of the young puts an additional strain on the ability of the attendants to perform the double duty of feeding the young and defending them from predators. Out of the 14 young produced by the four flocks under study, two (from Nest 3 of Flock 1A) did not survive beyond the first week after fledging, and two more (of Flocks 3 and 4) disappeared within two months after fledging. The post-fledging dependency period seems to be, then, the most critical one for the survival of the young, and also the one in which the helpers make a most significant contribution to the breeding success.

The social system of the Green Jays has been a key factor in their adaptation to the present habitat of secondary forests, grasslands, and coniferous plantations. The efficient system of defense of their nests, coupled with the opportunistic feeding habits and the flexibility of their diets, permit the jays to breed successfully in a variety of vegetation types, all of which are different in structure and composition from the original oak forest. By virtue of the same adaptations, the jays take advantage of certain temporarily super-abundant food sources that became available as a result of human interference with the original habitat. However, having evolved in the dense subtropical and montane forests, they probably have not developed yet the behavioral adaptations for flying across the relatively large open spaces that often intersect their territories. Further clearing of the secondary forests may create severe barriers against the dispersal into areas that may become available either by reforestation or natural regeneration.

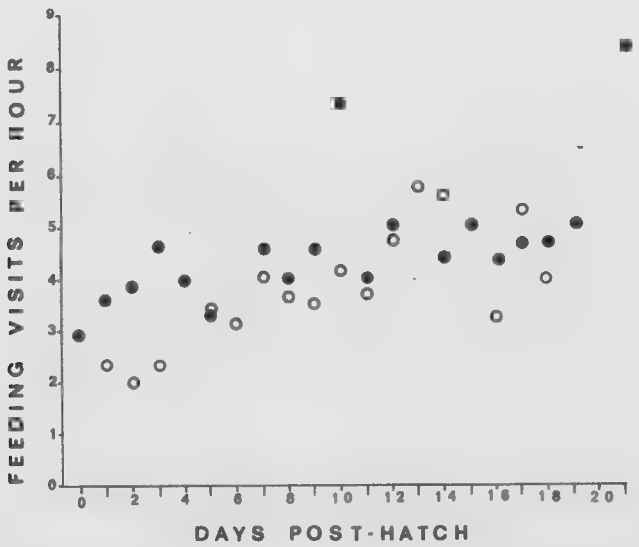


Figure 16. Feeding rates at Nest 2 of Flock 2 (black circles), and at Nest 3 of Flock 1A (clear circles).

TABLE 9

Numbers of Helpers and Breeding Success of Four Flocks of Green Jays

Flock	*Number of helpers*	*Number of fledglings*	*Survivors*	*Percentage of fledglings that survived*
Flock 1A	1	3	1	33.3
Flock 2	3	4	4	100.0
Flock 3	2	4	3	75.0
Flock 4	2	3	2	66.6
Total	8	14	10	71.4

A common origin of flocks in several species of jays is the retention of the young within the parental flocks (Brown, 1974). In seven of nine flocks of the Green Jay, I found immature individuals that were probably hatched during the previous breeding season. All the jays in this age class that were present in the study area acted as helpers in their respective flocks during the breeding season of 1973, and remained with their groups until the end of the study period. Similarly, all the young hatched during the breeding season covered by this study, and that survived to the end of the field period, were still attached to their parental flocks. Seemingly, young Green Jays do not disperse, but remain with their parents and help them raise the brood of at least one subsequent breeding season.

The age at which Green Jays first breed remains unknown. However, assuming that immatures are birds one year old or less, and that sexually inactive adults (of which there was at least one in each flock under observation, Figure 5) are between one and two years old, it follows that Green Jays do not reach sexual maturity until at least their third year of age. Nevertheless, the possibility exists that sexually inactive adults, the plumages of which I could not distinguish from those of the breeding birds, are actually sexually mature but unmated jays that remain in the flocks. If this is the case, the age of first breeding is probably two years.

Apparently dispersal does not usually take place by emigration of single individuals, or by exchange of members between flocks, but by splitting of flocks into sub-groups, one of which leaves the original territory. This observation, coupled with the altruistic behavior of the helpers in feeding nestlings not their own, points to the possibility of a high coefficient of genetic relationship between members of a flock. For the Mexican Jay, also a communal breeder, Brown (1974) estimated the coefficient of genetic relationship *(r)* among members of a flock to be 0.8. This high coefficient means that ". . . an altruistic jay would be more closely related to the young of a recipient flock member than to his own young if he were to mate at random outside the flock (in which case *r* to his own young would be close to 0.5)".

Based on his theory on the evolution of communal breeding, Brown (1974) predicted a set of characteristics to be found in communal breeders. My findings on the Green Jay confirm, at least in a preliminary way, some of Brown's predictions. In fact, Green Jays show delayed maturity, which in turn results in a low reproductive rate. The flocks are solid social units, the behavioral integration of which probably favors an increased survival rate. The rate of dispersal from the parental flocks is very small, and intruders are actively repelled by the entire flock. These features are characteristic of cooperative breeders at Brown's "kin-selection phase." To determine whether territories consistently differ in their productivity of young, and whether territories are actually handed down within the same lineage—supposedly the main advantage conferred by this type of social organization—requires long-term observations on a larger population.

Summary

Green Jays *(Cyanocorax yncas)* in the mountains around Medellin, Colombia move about in small flocks of three to nine individuals in a wide variety of habitats from grasslands with scattered trees to dense secondary forests and plantations of pines and cypresses. These flocks form discrete social units that defend stable territories the year around. There is a notorious lack of aggression among members of a flock, and allo-preening is a frequent form of social interaction. The boundaries of the flock-territory are defended by all the members, and overt aggression occurs frequently between members of different flocks during territorial encounters.

When under attack by avian predators (mainly Sharp-shinned Hawks), the members of a flock cluster together, and harass and attack the raptor every time the latter attempts to capture a jay.

Nesting activities begin in March shortly after the start of the rains, and all flocks have young out of the nest by the middle of June at the peak of the rainy season.

Flocks do not dissolve during the breeding season. A mated pair frequently leaves the rest of the flock for courtship feeding and allo-preening, but only for a few minutes. Nests are built mainly by the pair, but other members of the flock follow them around, occasionally obtaining nest materials. There is only one breeding pair in each flock.

Females lay four eggs on consecutive days and incubation probably begins after the third egg has been laid. The incubation period lasts 17 to 18 days. During the incubation period, females spend up to 98 percent of their time sitting tightly on the eggs and are attended at the nest by their mates. Other members of the flock start feeding the female toward the end of the incubation period.

From the day of hatching, all members of the flock cooperate in feeding the young. The helpers may contribute more than 50 percent of all the feeding visits. Female parents contribute a smaller proportion of the feeding visits than any other members of their flocks. All the jays in the flock also cooperate in nest sanitation. Helpers participate actively in scolding and attacking predators near the nest and guard the nest during inattentive periods of the female parent.

Young jays fledge between 19 and 22 days of age but, if disturbed, they may leave the nest at 17 days of age. The young continue to be fed by the parents and their helpers for at least 20 days after fledging. In defending the fledglings from potential predators, the flocks form mobbing assemblies that harass the intruders for extended periods, during which the young continue to be fed by flock members that move in and out of the assemblies.

Juvenile Green Jays apparently do not disperse from their parental flocks; they stay to serve as helpers at the nest for at least the following breeding season. Sexual maturity is probably delayed until their second year of age.

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SUNBATHING IN GREBES

ROBERT W. STORER, W. ROY SIEGFRIED, AND JOHN KINAHAN

Although sunbathing by birds is a well-known phenomenon (Kennedy, 1969; Mueller, 1972; Potter and Hauser, 1974), it has not been extensively studied, and the importance of solar radiation as a direct source of energy for birds only recently has been recognized (Hamilton, 1973; Ohmart and Lasiewski, 1971). In particular, sunbathing by grebes has rarely been reported (Bandorf, 1970:33; Edscorn, 1971:93; Rankin, 1947:40) and not well described.

In 1971 Storer and Siegfried met in southern Texas and discovered that each had observed sunbathing in grebes and had postulated a thermo-regulatory function for it. Storer's observations had been on the Least Grebe, *Tachybaptus dominicus,* in Texas and Siegfried's on the Dabchick *(T. ruficollis)* in South Africa. After his return to South Africa, Siegfried, assisted by Kinahan, collected quantitative data in the field to test the hypothesis and examined specimens of the Dabchick for the distribution of pigment in the skin and feathers. The receipt of several frozen Least Grebes and Pied-billed Grebes *(Podilymbus podiceps)* from Robert W. Dickerman permitted Storer to study the distribution of pigment in these species. This in turn prompted the senior author to make a survey of sunbathing in grebes based on fresh and preserved specimens, study skins, field notes, ciné films, and the literature. The interpretation of the resulting survey was aided considerably by Hamilton's (1973) ideas on color and energy relationships.

Although sunbathing is a frequent and easily observed behavior pattern in small grebes, it does not appear to have been reported for the Least Grebe and only casually mentioned, although well figured, by Bandorf (1970:17, 33) for the Dabchick. As far as we are aware, the relationship of sunbathing to skin and feather pigmentation in grebes has not been described.

Sunbathing in Three Grebes

Least Grebe

In sunbathing, these grebes sit on the water with the closed wings tilted up at an angle of 30 to 45 degrees and the white feathers of the lower back, flanks, and what appear to be under tail coverts spread (Figures 1 and 2). Least Grebes also expose a white patch at the back of the head, formed by white portions of the nape feathers. At other times these white areas are covered by dark feathers or the dark distal portions of overlying feathers. That this posture is a form of

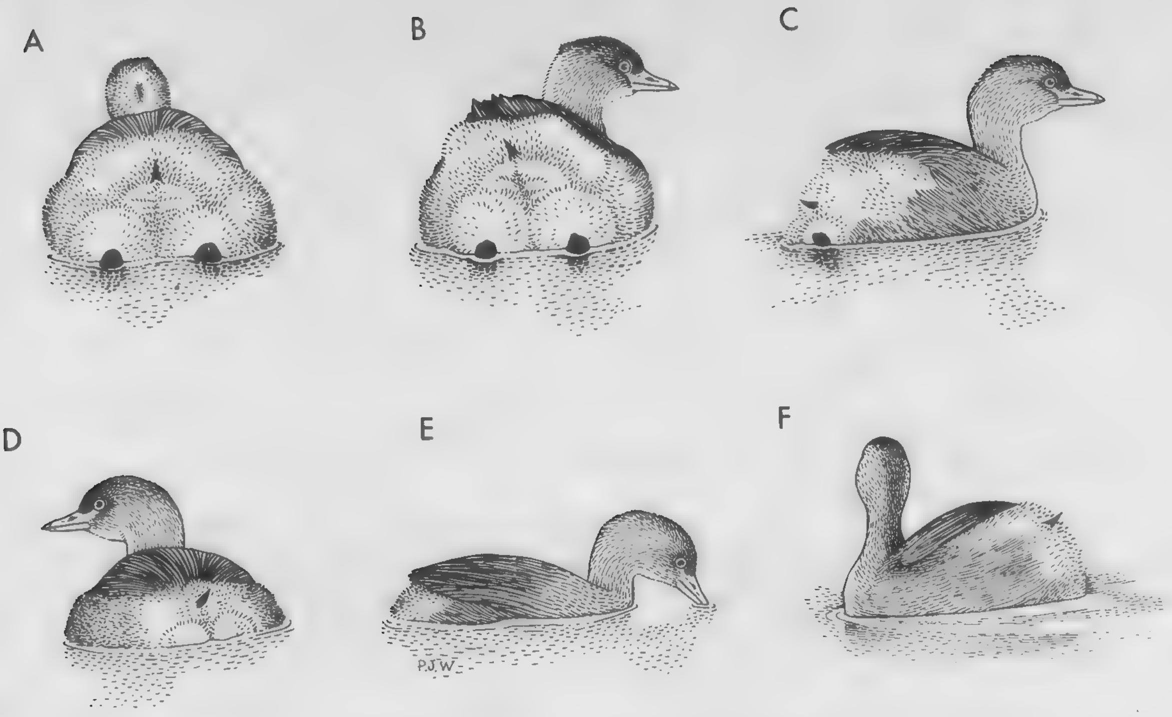

Figure 1. A-E, Sunbathing and pre-dive postures of Least Grebes, *Tachybaptus dominicus.* F, sunbathing Hoary-headed Grebe, *Poliocephalus poliocephalus.*

sunbathing is evident when a cloud obscures the sun and the grebe assumes the more usual swimming posture. It is also noteworthy that when sunbathing, the birds turn their tails toward the sun, a behavioral orientation that usually takes precedence over the almost universal avian habit of facing into the wind.

On one occasion when ducks, coots, and Pied-billed Grebes were facing into a fairly strong wind, Least Grebes nearby faced away from the wind (and sun), which strongly ruffled their scapulars. Between foraging dives, Least Grebes frequently sunned; but when the wind was strong they lowered their wings and back feathers and faced into the wind immediately before diving. Once, when there was a light overcast but strong shadows, the birds sunned and faced away from the sun. However, with a somewhat heavier overcast, they only partly spread the white feathers and apparently oriented at random. Storer did not observe sunning under heavy overcast.

Storer recorded sunbathing by Least Grebes on warm and cool days. On March 30, he recorded the daytime water temperature as 21°C at the pond on the Santa Ana National Wildlife Refuge, where most of his observations were made. This is presumably in the neighborhood of 19° below the body temperature of the birds. This temperature differential suggests that sunbathing may compensate for heat lost through the feet to the water as well as through the rest of the body. The universal habit of grebes of shipping one or both feet against the body and under the wings while resting (Figure 3) offers indirect evidence of the importance of heat loss through the feet to the water.

Examination of frozen specimens and pelts shows that the principal areas exposed during sunbathing are two patches of lax, silky white feathers extending from the axilla to the tail. In the Least Grebe, these feathers vary in length from approximately 10 millimeters anteriorly to 25 mm near the tail. The proximal fourth of the feathers is pigmented, as are the tips of the longest ones. The remaining portion is white. In the normal swimming posture, these white areas are covered by the folded wings, which are covered in turn by the long flank feathers. The latter measure approximately 45 mm in length and, except for

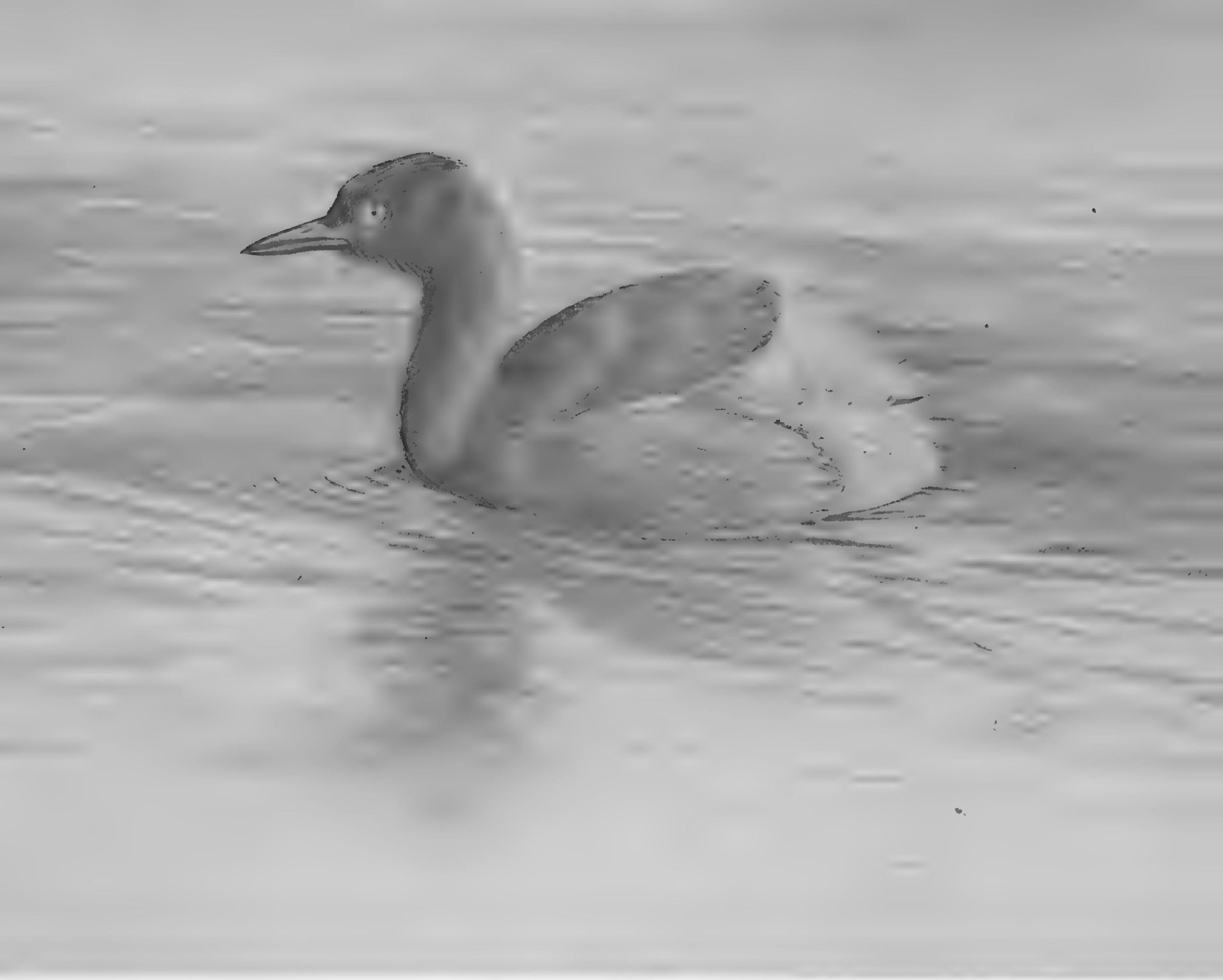

Figure 2. A Least Grebe in sunning posture. Drawing by Barry Kent MacKay.

the dark shafts, are pigmented for only the proximal five mm and the distal 15 mm. The two white patches are separated by the short feathers of the dorsal tract, which are brownish black for all but the posterior 20 mm, where they are white and thus connect with the white lateral patches. Posterior to the dense feathers of the underparts is another group of lax feathers which are spread during sunning. These feathers are approximately 30 mm long and are pigmented for the proximal and distal eight mm. The skin beneath all these dark-based white feathers is heavily pigmented in contrast to the rest of the skin. The fluffy white portion of the feathers presumably reduces heat loss through convection and yet can be penetrated by solar radiation, which is absorbed on the black skin and bases of the feathers. This pigmentation of the skin and feathers is shown diagrammatically in Figure 4.

In the Least Grebe, the feathers of the nape that are raised in sunbathing are approximately 11 mm long, the proximal two mm and the distal five mm being pigmented and the central four mm white. The skin beneath these feathers is more intensely pigmented than that of the throat, but by no means as dark as that of the lower back (Figures 1A and 4).

Dabchick

Siegfried and Kinahan collected data on orientation of Dabchicks in winter and summer at an eight-acre (three hectare) farm dam near Stellenbosch

(33° 57' S Lat., 18° 50' E Long.), South Africa. From local sunrise (08:00) to sunset (18:00) on several days in July 1974, they recorded behavior and orientation every ten minutes for 15 out of a flock of 80 birds. The sample consisted of every fifth bird encountered while making a visual scan of the flock. For recording orientation, the compass was divided into half quadrants, each centered on a cardinal point. The observer remained in a fixed position and used fixed landmarks in determining the directions in which the birds faced. Air and water temperatures were taken. In December 1974, a similar set of data was taken.

The results show that on clear, windless days, the birds tend to face away from the sun and to assume the sunbathing posture (Figure 5). This presumably enhances penetration of sunlight to the dark skin beneath the white feathers. Orientation away from the sun was more frequent on cloudless days in winter (July) than on overcast days or on cloudless days in summer (December) when water temperatures were nearer those of the air (Tables 1 and 2). The sunbathing posture was assumed more frequently on cloudless days than on completely overcast days (Table 3). On clear days birds tended to remain in the sunbathing orientation for approximately 10 seconds between the dives of a foraging bout. A bird also tended to dive in the same general direction as its initial orientation on the surface. Half of these dives occurred within the 45-degree segment encompassing the direction in which the bird originally faced (Figure 6), and occurred whether the birds faced toward, or away from, the sun. Thus, 88 percent of 77 dives were made in the direction of their original orientation toward the sun, and 85 percent of 162 dives were made in the direction of their initial orientation away from the sun. This suggests that orientation is not related to foraging efficiency, for example, in providing a better view of potential prey by having the light behind the bird.

Eared Grebe

The "high-sterned" look of the Eared Grebe *(Podiceps nigricollis)* is a well-known field mark of the species (Hoffmann, 1927:8; Peterson, 1941:4), but we know of only one brief attribution of this posture to sunning. Edscorn (1971:93)

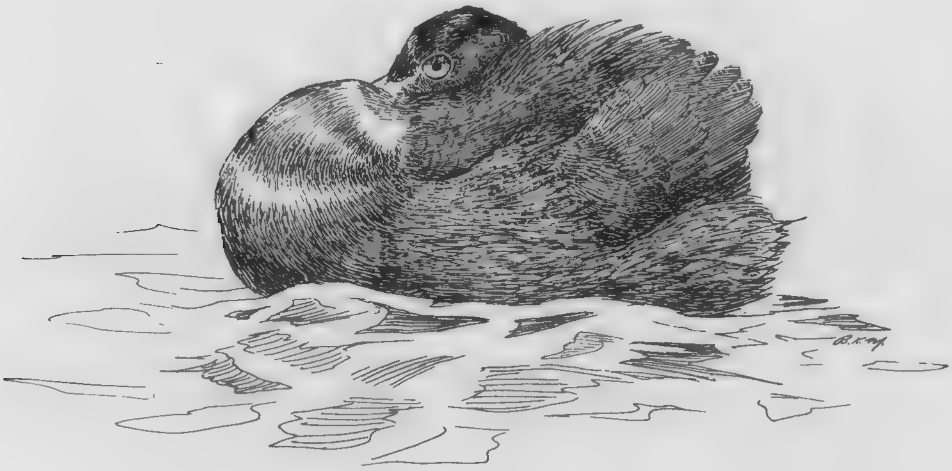

Figure 3. A Least Grebe in resting posture. Drawing by Barry Kent MacKay.

TABLE 1

Mean Air and Water Temperatures[1] on Cloudless, Windless Days in July and December

Hour	*Air temperatures (centigrade)*		*Water temperatures (centigrade)*	
	July	*December*	*July*	*December*
05:00		18.2		15.6
06:00		21.1		16.9
07:00		22.8		20.7
08:00	7.5	23.5	10.2	22.0
09:00	9.6	27.2	11.8	22.1
10:00	17.0	27.4	12.8	23.7
11:00	20.0	27.7	13.8	24.0
12:00	21.0	27.9	14.2	24.1
13:00	24.0	28.3	14.8	24.9
14:00	23.4	27.2	14.5	25.0
15:00	23.6	25.8	14.8	23.4
16:00	20.8	25.7	14.2	22.9
17:00	17.4	19.5	13.8	16.0
18:00	16.4	15.0	13.4	14.1
19:00		14.6		12.3

[1] Air temperatures were made in the shade, and water temperatures were taken 10 cm below the surface. Temperatures were recorded at fifteen-minute intervals.

wrote that on emerging from a dive on cold days an Eared Grebe ". . . instantly turned its high rump to the sun. We wondered if this afforded greater warmth." In the late morning of 6 December 1973, L.C. Binford and Storer watched four Eared Grebes on Lake Merced, San Francisco, California. Two, which were foraging near the north shore, assumed a sunning posture like that of a Least Grebe and faced away from the sun immediately on emerging from a dive. Presently, two others swam toward the first two. Their course took them away from the sun, and they were in the sunning posture, in spite of a light stern wind. Presently, one of the first two swam toward them (and the sun) but did not adopt the sunning posture.

Just prior to submerging, diving birds depress the plumage. This expels air trapped in it and thus reduces buoyancy. For some time, Storer thought that depressing the plumage from the high-sterned posture just before diving might be an exaggerated intention movement, which could serve a signal function in this highly gregarious species. This might still be true; but the pigmentation of the skin of the back and the black-based white feathers lying over this pigment, taken with the above observations, are good evidence that the primary function of the high-sterned posture in this species is heat absorption.

A Survey of Sunbathing in Grebes

Pelts or frozen specimens of *Tachybaptus dominicus, Podilymbus podiceps, Podiceps auritus,* and *P. nigricollis* were examined for heavily pigmented skin on the back. In addition, the skin of this area was removed from fluid-preserved specimens of all the remaining species except *Tachybaptus pelzelnii* and *Poliocephalus rufopectus* to determine the presence or absence of this type of pigmentation. Feathers from the back of all species were mounted on microscope slides

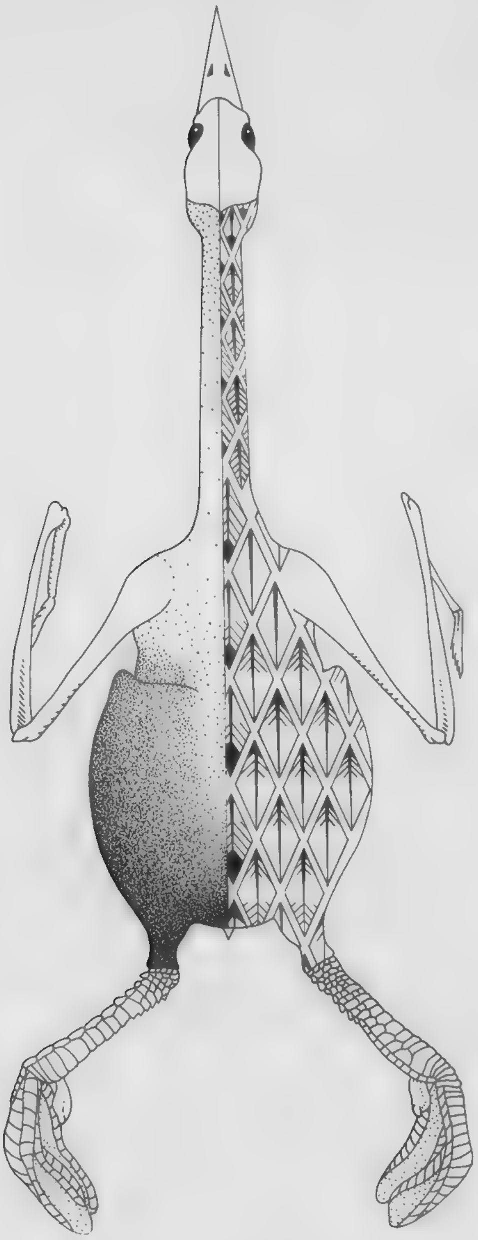

Figure 4. Least Grebe, showing pattern of pigmentation on skin of back (lower half) and on feathers (top half).

and checked for heavily pigmented bases. The results are shown in Table 4, in which the species are listed in order of increasing size. Mean weights for most species were calculated from data on museum labels. Additional data for *Tachybaptus ruficollis* and *T. rufolavatus* from Voous and Payne (1965) and for *Rollandia chilensis* and *R. microptera* from Niethammer (1953) were included in the calculations. The data for *Podilymbus gigas* are from LaBastille (1974). No weight data were available for *pelzelnii,* but on the basis of wing measurements (Voous and Payne, 1965), it is slightly larger than the Madagascar population of *ruficollis.*

In addition to the observations of *ruficollis, nigricollis,* and *dominicus* presented earlier, Storer observed that individuals of *Tachybaptus novaehollandiae* assume the sunbathing posture and face away from the sun. He has also observed or filmed the sunbathing posture in *chilensis, microptera, poliocephalus, rufopectus, Podiceps occipitalis,* and *P. taczanowskii,* but has no behavioral evidence that adults of *podiceps, gigas, auritus, Podiceps grisegena, P. cristatus, P. major,* or *Aechmophorus* *occidentalis* sunbathe, although Rankin (1947:40) reports this in small chicks of *cristatus.*

Discussion

Effects of Size and Elevation

Potential heat loss is greater for small animals than for large ones because a small object has a larger surface area per unit of volume ($SA \sim V^{2/3}$). Furthermore, small birds tend to carry thinner insulative layers than larger ones (Kendeigh, 1970). Hence, at a given difference between body and environmental temperatures, a small animal loses heat more rapidly per unit of body weight than a large one. For small homeotherms exploiting an aquatic environment, this relationship between heat loss and body size may become critical. In diving birds like grebes, additional insulation in the form of an increased amount of air trapped in the feathers would increase buoyancy, which would reduce efficiency of locomotion underwater. In fact, the birds expel part of the trapped air from the feathers just before submerging. Hence the maximal insulation afforded to diving birds by their plumage is probably severely limited.

Small animals, particularly aquatic homeotherms, require more energy per gram of body weight than large animals. Energy obtained directly from solar radiation can reduce the amount of energy required from food and also the amount expended in obtaining food. These arguments indicate that the selective advantage of using external energy sources like the sun is inversely proportional to the size of the animal and may be accentuated in aquatic animals. In grebes, sunning is used in all the small species with a mean weight of 350 grams or less; and only two species with greater mean weights are known to sunbathe (Table 4).

These exceptions are *taczanowskii* and *microptera,* both confined to Andean lakes between 12,000 and 13,500 feet (3,658 and 4,115 meters) elevation. Hamilton (1973:39) points out ". . . that an animal species with a center of distribution at relatively high altitudes in relatively clear regions will be particularly subject to selection for behavioral and morphological adaptations which will put this

TABLE 2

The Frequency[1] of Body Orientation by Dabchicks in Relation to the Position of the Sun on Cloudless and Completely Overcast, Windless Days

Behavior	*Cloudless, December*[2]		*Cloudless, July*[3]		*Overcast, July*[3]	
	Facing sun	*Facing away from sun*	*Facing sun*	*Facing away from sun*	*Facing sun*	*Facing away from sun*
Resting	43	57	15	85	54	46
Diving	44	56	33	67	55	45
Preening	33	67	23	77	52	48
Swimming	46	54	43	57	61	39

[1] Expressed as a percentage.

[2] Based on one fifteen-hour set of observations embracing 575 instantaneous determinations of orientation and behavior.

[3] Based on one ten-hour set of observations embracing 855 instantaneous determinations of orientation and behavior.

TABLE 3

The Frequency[1] of Sunbathing Posture by Dabchicks in Relation to the Position of the Sun on a Completely Overcast Day in July and Cloudless, Windless Days in July and December

Behavior	*Overcast, July*[2]			*Cloudless, July*[3]			*Cloudless, December*[4]		
	Facing sun	*Facing away from sun*	*Number of determinations*	*Facing sun*	*Facing away from sun*	*Number of determinations*	*Facing sun*	*Facing away from sun*	*Number of determinations*
Resting	4	11	396	67	87	350	56	61	181
Diving	3	4	94	10	10	242	74	28	133
Preening	7	15	30	73	88	27	43	55	57
Swimming	3	8	61	41	55	81	75	55	127

[1] Expressed as a percentage.

[2] Based on a ten-hour observation period embracing 581 instantaneous determinations of orientation and behavior.

[3] Based on a ten-hour observation period embracing 700 instantaneous determinations of orientation and behavior.

[4] Based on a fifteen-hour observation period embracing 498 instantaneous determinations of orientation and behavior.

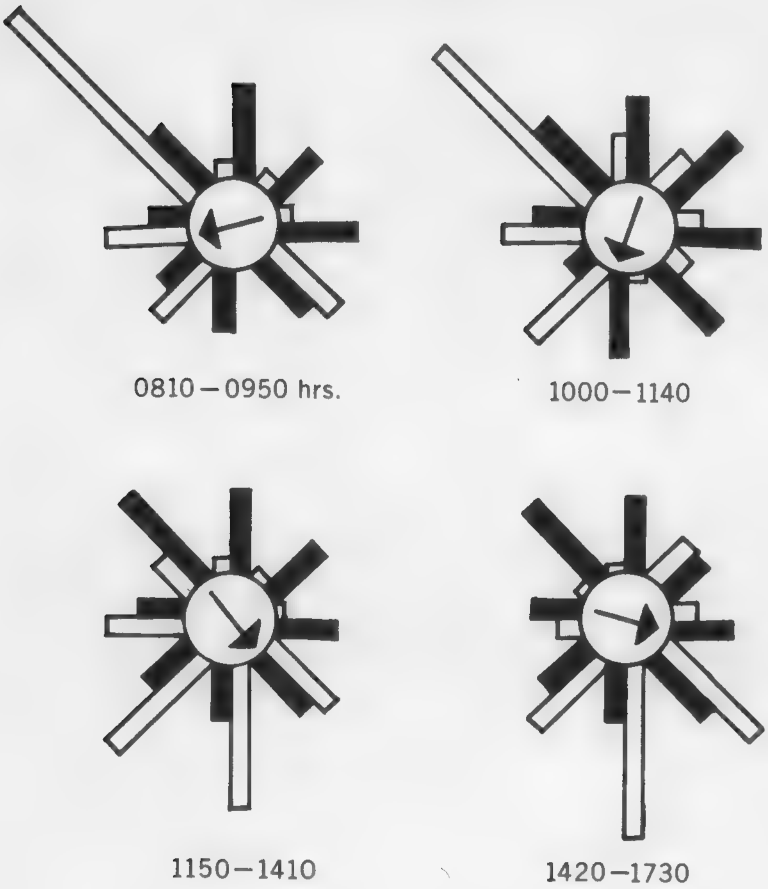

Figure 5. Dabchick, *Tachybaptus ruficollis,* orientation with respect to the sun in midwinter. Arrows show direction of the sun's rays at midpoints of the indicated time intervals. Shaded columns indicate overcast sky; orientation random. Clear columns indicate cloudless sky; birds tend to face away from sun. Figure is based on two sets of ten-hour observations involving 855 instantaneous determinations of orientation.

[solar] energy source to use." By interpolation from Hamilton's (1973:41) table, the amount of radiant energy at the elevations at which these two species live is approximately 1.4 times that at sea level. The closest relatives of these species are *occipitalis* and *chilensis,* respectively, both small, sunbathing forms that occur from sea level to over 14,000 feet (4,267 meters) in the Andes. It is also noteworthy that the South American species *(podiceps* and *major)* that lack sunbathing behavior are not found at elevations higher than 9,000 feet (2,743 meters) and 4,000 feet (1,219 meters), respectively. Thus sunbathing in the presumed ancestral forms may be a preadaptation for year-round life at high elevations.

Function of Sunbathing

Some of the suggested functions of sunbathing have been summarized by Kennedy (1969:251-254). These include heat absorption; increasing the mobility

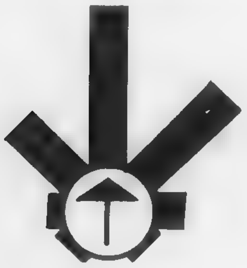

Figure 6. The frequency of diving direction of Dabchicks with respect to initial body orientation and expressed as a percentage. Figure is based on 200 observations at all hours of the day. The arrow indicates the initial body orientation.

TABLE 4

The Occurrence of Sunbathing and Associated Pigmentation in Grebes

Species	*Mean weight (grams)*	*Pigment on skin*	*Black base to back feathers*	*Sunbathing posture*
Least Grebe *(Tachybaptus dominicus)*	131	present	present	present
Alaotra Grebe *(Tachybaptus rufolavatus)*	189	present	present	unknown
Red-throated Dabchick *(Tachybaptus ruficollis)*	192	present	present	present
Madagascar Grebe *(Tachybaptus pelzelnii)*	unknown	unknown	present	unknown
Australian Dabchick *(Tachybaptus novaehollandiae)*	207	present	present	present
Rolland's Grebe *(Rollandia r. chilensis)*	247	present	present	present
Hoary-headed Grebe *(Poliocephalus poliocephalus)*	249	present	present	present
New Zealand Dabchick *(Poliocephalus rufopectus)*	253	unknown	present	present
Silver Grebe *(Podiceps occipitalis)*	323	present	present	present
Eared Grebe *(Podiceps nigricollis)*	334	present	present	present
Pied-billed Grebe *(Podilymbus podiceps)*	396	absent	absent	absent
Horned Grebe *(Podiceps auritus)*	405	absent	absent	absent
Taczanowski's Grebe *(Podiceps taczanowskii)*	427	present	present	present
Atitlan Grebe *(Podilymbus gigas)*	699	absent	absent	absent
Flightless Grebe *(Rollandia microptera)*	706	present	present	present
Red-necked Grebe *(Podiceps grisegena holbollii)*	990	absent	absent	absent
Great Crested Grebe *(Podiceps cristatus)*	1,042	absent	absent	absent
Western Grebe *(Aechmophorus occidentalis)*	1,087	absent	absent	absent
Great Grebe *(Podiceps major)*	1,478	absent	absent	absent

of ectoparasites, making them easier to remove by preening; drying the plumage; vitamin D production; some unspecified role in molting; and increasing the production of secretion in the oil gland. More recently, Potter and Hauser (1974) have related anting and sunbathing to molting in North Carolina land birds. Grebes that sunbathe differ from most or all other birds which do so in two respects: (1) sunbathing is not confined to a few scattered periods but occurs most of the time that the birds are on the surface of the water and the sun is shining; and (2) there appears to be no regular preening immediately after sunning. Because of the length of time spent sunbathing, the lack of preening after each bout, and the dark pigmentation of the skin and feather bases, it is probable that sunbathing in grebes functions primarily, if not wholly, in heat absorption. The infrequency of preening after sunbathing rules out the possibility of this behavior serving to aid in the removal of ectoparasites. The white feathers spread at the inception of sunbathing appear dry and fluffy, one reason why drying the plumage can be ruled out. There is also a second reason. The peculiar, coiled barbules on the contour feathers of grebes, described and figured by Chandler (1916:301) resemble those on the belly of male sandgrouse with which water is brought to the young (Cade and Maclean, 1967). In grebes, the coiled barbules are found on the outer three-fourths or more of the feathers, the proximal part being downy. The latter maintains at least a thin layer of air next to the skin, whereas the outer portion becomes wet through absorption of water within the coils of the barbules. The trapped air has obvious insulative value. The adaptive value of the water trapped by the barbules has not been demonstrated, but George S. Bakken (pers. commun.) suggests that the surface tension of the water film thus trapped may form a skin-like barrier which prevents penetration of water to the air space beneath. If water retained in the feathers is of value in diving and the primary function of sunbathing were to dry the feathers, sunbathing in the brief intervals between dives presumably would not occur.

Summary

In sunbathing, grebes raise the black-based, white feathers of the back, and face away from the sun, exposing the heavily pigmented skin to the sun's rays. This behavior and pigmentation are characteristic of small species and of two species confined to high Andean lakes; they are not found in large lowland species. We consider sunbathing in grebes to be an adaptation for utilizing solar energy.

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Drawing of Taczanowski's Grebe by Barry Kent Mackay

Golden Eagle, *Aquila chrysaetos.* Painting by James E. Coe.

BIOLOGY OF THE HARRIS' HAWK IN SOUTHERN ARIZONA

WILLIAM J. MADER

Photographs by the author

The Harris' Hawk *(Parabuteo unicinctus superior)* occurs locally as a common resident in parts of southern Arizona. Short notes have been published, but generally the Harris' Hawk can be considered an unstudied species. The purpose of this paper is to report my findings on Harris' Hawks and discuss some of the unknown aspects of their biology. An important result of this study was the observation that Harris' Hawks nest not only in pairs (twosomes) but also in trios (threesomes). Observations from the blind at three such nests indicated that the extra hawk served as a nest helper by feeding the chicks and/or supplying prey at the nest.

Brown and Amadon (1968) give the range of the subspecies *P. u. superior* ". . . as suitable lowland areas in southeastern California, southwestern Arizona, south in western Mexico, including Baja California, to Nayarit." They state that *P. u. superior* is the largest of the three subspecies of Harris' Hawks.

The Study Areas

Harris' Hawk populations in Pima and Pinal Counties occur exclusively in the flatlands of the Lower Sonoran life zone. The Sonoran Desert is the hottest of the southwestern deserts with the biseasonal rainfall appearing primarily in the winter (Lowe, 1964). Harris' Hawks occur here where the primary understory bush is the triangle bur-sage *(Franseria deltoidea)* and the important trees and cacti are the palo verde trees *(Cercidium microphyllum* and *C. floridum),* ironwood tree *(Olneya tesota),* mesquite tree *(Prosopis juliflora),* saguaro cactus *(Carnegeia gigantea),* prickly pear cactus *(Opuntia* sp.), and the cholla cacti *(Opuntia fulgida* and *O. Bigelovi).*

Harris' Hawks ranged over elevations of approximately 550 to 885 meters. Annual temperatures 5.6 kilometers from the study area averaged 68 degrees fahrenheit from 1971 to 1974. Annual precipitation in these years averaged 31.3 centimeters.

Methods

In February 1971 I initiated a preliminary investigation on the Harris' Hawk population in Pima and Pinal Counties, Arizona. In a study area 38 square kilometers in size I carried on intensive studies of Harris' Hawks from September 1971 to June 1973. Incidental investigations were made on Harris' Hawks from 1969 to 1975.

By trapping and making weekly circuits by car in the study area, I recorded winter distribution, abundance, and group composition of wintering Harris' Hawks. Hawks trapped with Bal-chatri traps (see Berger and Mueller, 1959) were measured and sexed in the field by using comparative measurements of 73 museum specimens. Females were about one-third larger than males. Fourteen females (wing chord 362-385 mm, mean = 375; weight 918-1,203 grams, mean = 1,047) and 37 males (wing chord 318-360 mm, mean = 335; weight 634-877 grams, mean = 725) showed no overlap in wing and weight measurements in my study.

By car and on foot, I studied nest-site preferences, clutch sizes, nestling success, and comparative yearly nest success both in the study area and elsewhere. I measured nest heights by connecting 1.5-meter poles together, and measuring to the nearest 15 cm. Banding of Harris' Hawk nestlings was accomplished by use of an extension ladder. Measurements of nestlings from which I plotted a growth curve were taken once every four days at a nest with two adults in 1973.

A wooden tower 4.8 meters high, with a small blind on top, was constructed 18.6 meters south of a Harris' Hawk nest in 1973. The birds at this nest included two adult males, one with a band and the other with distinctive plumage, and a color-banded female. I observed this nest from the blind on 26 days for a total of 164 hours, of which 157.6 hours were during the nestling phase. I observed the nestlings from 24 March, when the young were less than 24 hours old, to 4 May. Observations were aided by a 30X spotting scope. I compiled daily activity charts for the adults and young at the nest and nearby areas. High winds shortened watch-periods on some days. The duration of continuous observations ranged from one hour to approximately 10 hours, with an average of six hours and five minutes. Of the 164 hours, 48 percent were in the morning hours. In 1974 I made part-time observations on this same trio from a tower blind for 87 hours, from 26 July to 20 August.

I spent approximately 47 hours in tower blinds at two other Harris' Hawk nests in 1972. Although I gathered useful information about the trios at these two nests, it was largely preliminary work toward the in-depth blind observations of 1973.

Winter Populations

Excluding recaptured nestlings, I trapped 31 males and 11 females (2.8 males per 1.0 female) of which nine males and three females were immatures. However, this may not be an accurate indication of the true sex ratio, since differences may exist between male and female Harris' Hawks regarding trap susceptibility.

Car censuses in 1972 and recaptures and sightings of color banded Harris' Hawks indicate that many immature and adult Harris' Hawks in southern Arizona are non-migratory. At least nine hawks banded the previous year, or having distinct features by which they could be identified, were known to be present in the study area in the winter 1972-1973. Several banded immature and adult hawks were not recaptured and were consistently sighted during the winter months in the study area in 1972-1973. In two instances outside the study area, adults trapped in the winter nested in the same area the following spring. I commonly observed Harris' Hawks in small groups in the winter (Table 1).

In the winter of 1971-1972, approximately 25 to 30 Harris' Hawks resided in the study area. Some movement of hawks inside and outside the study area may have led to changes in numbers and individuals during the winter.

An important segment of wintering populations of Harris' Hawks in southern Arizona consist of family groups (Table 1). I trapped both banded and unbanded immatures accompanying adults on four different occasions. The presence together of unbanded and banded immatures from separate nests indicates that families join together for an indefinite period of time. I found no evidence of band losses among Harris' Hawks.

I witnessed evidence of juvenile dependence on adults on a number of occasions. Immatures gave the begging call, a characteristic call for food in the nestling period, eight months after they had fledged. In one case an immature

Harris' Hawk, *Parabuteo unicinctus.* Drawing by Tony Angell.

A pair of Harris' Hawks, drawn as observed in a captive situation. Woodland Park Zoo, Seattle, Washington. Scratchboard by Tony Angell.

TABLE 1
Group Sightings of Harris' Hawks in a
Study Area[1] in Southern Arizona

	Number of hawks in group						*Totals*		*Average number of hawks per group*
	1	*2*	*3*	*4*	*5*	*6*	*Number of hawks*	*Number of groups*	
Number of groups sighted:									
October 1971 to January 1972 (22 field days)	11	11	12	8	3	0	116	45	2.6
October-November 1972 and January 1973 (11 field days)	5	5	2	6	0	1	51	19	2.8

[1] Size of study area equals 38 square kilometers.

hawk with a foot missing was seen always in the presence of three adults in one locality. I last saw this immature on 4 February 1973, 104 days after first sighting it and only about 30 days before this trio started to lay eggs. Another immature, with one foot totally paralyzed, was trapped in the presence of another immature and an adult male on 12 November 1973. Each of these crippled immatures gave constant begging screams in the presence of an adult. It appears unlikely that they could have existed for so long without receiving prey from other Harris' Hawks.

I witnessed only one prey exchange in a winter Harris' Hawk group. An immature hawk in a tree allowed another immature to take a partially eaten Gambel's Quail *(Lophortyx gambelii)*.

Nesting Behavior, Productivity, and Ecology

One of the major results of the study of nesting behavior was the observation that polyandry exists among some percentage of the population. Aspects of this breeding system are discussed in sections below.

Seasonal Timing of Breeding

Harris' Hawks nested from February to October. Most breeding females laid eggs in early March while hatching centered around the middle of April, and fledging the last half of May (Figure 1). The earliest egg-laying I recorded was on 10 February and the latest approximately 25 August (for a second clutch of eggs). Latest fledging date was about 26 October. I defined fledging as the time at which the chicks were unable to fly well but left the nest intermittently to perch in nearby limbs. Harris' Hawks usually fledged at about 40 days of age.

The dates of egg-laying for two renestings in 1972, were approximately 16 April and 20 May, or about 54 and 67 days, respectively, after the first egg in each of the initial clutches was laid. Egg-laying occurred at another renesting on about 15 April.

Pache (1974) found two nests that fledged young on 15 September in southeastern New Mexico. At a nest in Texas, the first Harris' Hawk nestling left the nest on 23 or 24 October and the second nestling on 10 or 11 November (LeSassier and Williams, 1959).

Courtship and Copulation

I witnessed what I presumed to be courtship flights on only two occasions. An adult male went into an 80- to 90-degree stoop with folded wings and outstretched feet from an altitude of about 150 to 200 meters. The flights were typical of courtship stoops common to so many hawks (Brown and Amadon, 1968), and each ended in an upward swooping glide to the back of an adult female on top of a saguaro where copulation followed immediately. Courtship flight was not always a prerequisite to copulation. At an intensively studied nest I observed identical flights by two males in the presence of the single female during the nestling phase. The female either perched on a saguaro during such flights or joined the male in the stoop. On several occasions all three adult hawks stooped together for 30 meters or more, either in a loosely formed group three to six meters apart or in a single file.

I witnessed copulation on 13 occasions. The duration ranged from 5 to 170 seconds and averaged 28 seconds. The male often maintained his position on the female's back for relatively long periods of time. I estimated that in copulations of over one minute, only 30 to 50 percent of the mounting time was actually spent in copulation. Two copulations were accompanied by "chirp" or alarm calls. Of the 13 observed copulations, eight occurred on saguaros, four on telephone poles, and one in a tree. Others have witnessed Harris' Hawks copulating on the ground (Parmelee and Stephens, 1964), on a mesquite bush, and on a fence post (Pache, 1974).

On one occasion the female had prey when copulation occurred. In this instance, the female was 15 meters from the nest in an ironwood tree when one of the two adult males in the trio landed beside her and mounted. The other male was incubating on the nest. Generally, copulations proceeded smoothly with no hostile interactions displayed by the birds involved.

Whether both males in trios usually copulate with the female is not known. However, in cases at two nests both adult males of nesting trios copulated with the same adult female. In the Galapagos Hawk *(Buteo galapagoensis)*, it is not uncommon for more than one male to copulate with the same female in a given season (de Vries, 1973).

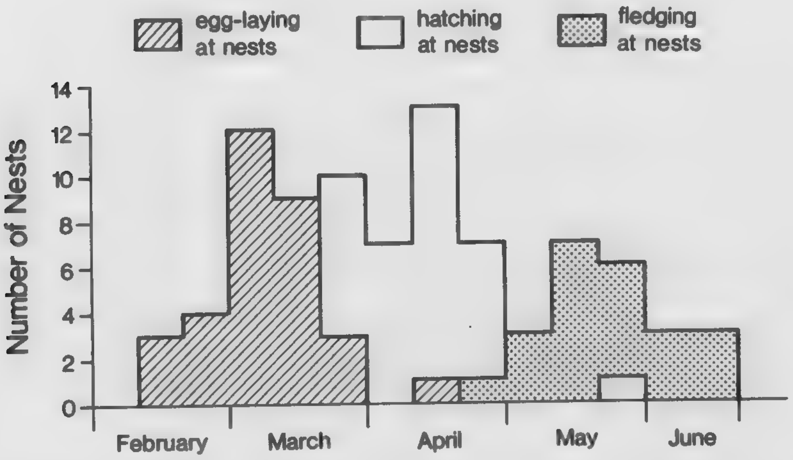

Figure 1. Breeding cycle of the Harris' Hawk in southern Arizona, as observed from 1971 to 1975, showing peaks and spreads for major events in the cycle. Only first clutches of the year are represented in the diagram.

Nest Building

I observed nest building at three nests. In two instances a trio presided over the nest site. At one site I saw only the female and one of the two males participate in nest building when observed for 165 minutes on two successive mornings. The female did almost all of the nest building during this period, bringing in dead sticks obtained from the ground (three sticks) and broken off from trees (three sticks). The sticks were carried in the bill (five times) or in the feet (once). In comparison, one male flew to the nest twice, once with a small dead stick in his bill that he had broken from a dead tree. The female gathered sticks within 90 meters of the nest, whereas the male flew about 530 meters to obtain his contribution.

At the intensively studied nest, I saw the adults search for sticks eight times. On five of the eight occasions, the hawks were successful in locating a stick and left the searching site carrying it in the beak. Of the eight, six were by Male 1 and two were by the female. In only one case was the stick brought to the nest and this was by the female. The other sticks that were picked up were dropped enroute. On two other occasions Male 1 and the female each brought in a stick but it was not known where or how they got them. Six of the eight stick searches were in trees, whereas two were on the ground and all occurred less than 30 meters from the nest.

At another nest, I watched nest building by two adults, presumably one female and one male. Both adults brought in sticks picked up off the ground approximately 30 to 60 meters from the nest. I could not determine if one or both hawks broke off any sticks from nearby trees. No calls of any kind were given by the birds during nest building activities.

Some Harris' Hawks in the study area began building nests about 36 days before laying eggs. However, I once saw an adult carry a stick to a nest in November and on another occasion found sticks that had been placed in the crotch of a saguaro by Harris' Hawks in December. It was not unusual for a pair or trio of hawks to build or repair as many as four different nests for occupancy, although other trios might build or repair only one nest.

The bulk of the nests varied according to the nest site. Saguaro nests were generally larger than tree nests because of the amount of space to be filled between the saguaro limbs. Nest material included dead sticks from red-gum eucalyptus *(Eucalyptus camaldulensis)*, ironwood, yellow palo verde, blue palo verde, and dried supports or "ribs" from dead saguaros.

The nest depression was approximately three to four centimeters deep at the time of egg-laying. The nest lining consisted of fresh sprigs from red-gum eucalyptus, aleppo pine *(Pinus halepensis)*, triangle bur-sage, pieces of dead cholla cacti, and unidentified grass and weeds. Unnatural material found in the nests included pieces of plastic, cloth, and newspaper. In some nests, I found prey remains prior to egg-laying, indicating that Harris' Hawks sometimes use new or rebuilt nests as feeding platforms.

Egg-laying and Incubation

Harris' Hawks lay white eggs (Figure 2). Six clutches had an average incubation period of 35 days with a range from 33 to 36 days. A seventh clutch was incubated for an unusually long period of 44 days. I consider the duration of incubation only approximate, because data on the laying of the first egg were not always known—nor, therefore, the intervals between the laying of eggs. Judging from the hatching times, incubation appeared to begin in some clutches

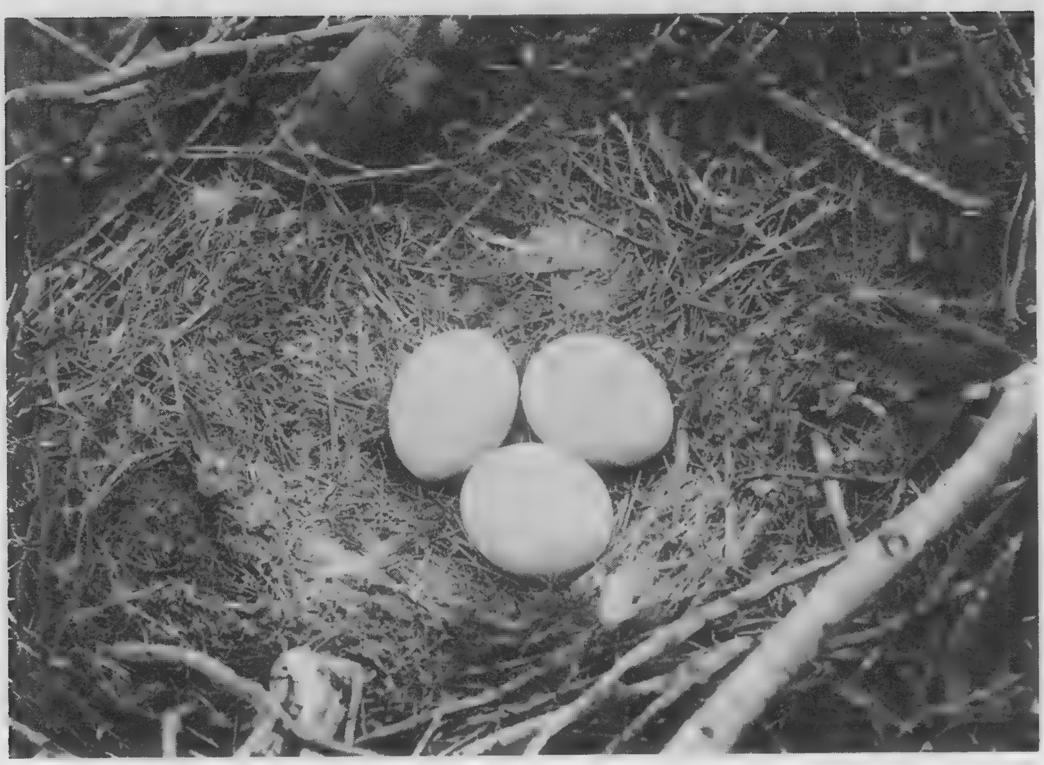

Figure 2. Nest of Harris' Hawk with eggs.

with the first egg, while in others it may have begun with the second, third, or fourth egg.

The estimated date of the start of egg-laying at the intensively studied nest was 17 February 1973. I spent only one day (from 09:00 to 15:30 hours) observing this nest during incubation, and it was three days prior to hatching. The longest attentive period by the hawks during incubation ran five hours and 51 minutes. The amount of time that adults spent on the nest varied from 19 to 102 minutes (mean = 60). On three occasions, an adult hawk took the place of another incubating adult at the nest, the change-over lasting only about 10 seconds. Once, when the incubating adult left the nest, another bird, or the same one, returned two minutes later and began incubating. On another occasion, the female brought a dead stick to the nest in her bill and exchanged places with the incubating male. Neither adult brought prey to the nest during incubation. However, in one instance the female left the nest and received prey from one of the males on top of a saguaro, 156 meters away. The male rendered "chirp" calls prior to the female's departure from the nest. Although not observed at this nest, I saw adults standing on nests shading the eggs on hot sunny days instead of incubating them. De Vries (1973) observed this same behavior in the Galapagos Hawk.

The female and at least one male at the intensively studied nest shared incubation. I could not determine whether both males participated in incubation. At one Harris' Hawk nest, presumably with a pair, Hensley (1959) observed only the female incubating. Bent (1937) states that both sexes share incubation. In a Galapagos Hawk trio (two males and one female), all three birds participated in incubating the eggs (de Vries, 1973).

Productivity

Fifty active Harris' Hawk nests, found from 1969 to 1973, produced 148 eggs and averaged 2.96 eggs per nest (Table 2). Clutches were checked two or more times at 42 (84 percent) of the nests to determine the final clutch size. I sexed one hundred seven hawks as nestlings, 56 males and 51 females.

I was unable to check some Harris' Hawk nests late in the nestling stage to see if the young had fledged. For this reason, and to simplify matters for discussion, a nest was considered successful if a chick was raised to an age of at least 28 days. Actual nest success and number of nestlings produced may be slightly lower than figures I report here. Thirty-four (68 percent) of the 50 nests were successful and averaged 1.60 chicks per active nest (Table 3). I found no evidence to indicate that my visits to nests contributed to nest failures or mortality of the young. Causes of nesting failures could be determined only for three nests. At two nests evidence indicated that the chicks were probably removed by human intruders. At the other nest, bullet holes in the nest and surrounding limbs indicated that the single nestling was probably shot.

I recorded three renestings after the destruction of the first clutches from undetermined causes, and all were successful. The adults built the new nests 400 to 960 meters from the old ones.

Double Clutches

I observed five cases of double clutching by Harris' Hawks. Three involved adult pairs and the other two the same adult trio. One nest occupied by a pair was found 13 March 1974 with four eggs, from which three young fledged. I found a newly rebuilt nest approximately 1,600 meters from this nest on 2 September with three newly hatched young; all the young fledged. In this same nesting range in 1975, a pair with a set of four eggs (2 March) raised one nestling. On 5 September, I found a recently used nest approximately 300 meters away and two fledged young in nearby trees. Because these nests were so close together and well separated from nearby nesting ranges, it seems reasonable that the same hawks were involved in both nests, if not both years. Another pair laid a set of three eggs (18 March) that produced one fledgling. The female laid a second set of four eggs in the same nest about 87 days after the completion of the first clutch and while the young hawk from the first clutch remained in the nest, still unable to fly well. The second clutch yielded one nestling. In 1974 a trio laid an initial clutch of four eggs (2 March) in a saguaro nest that fledged three young. On 18 July a new nest was found in a palo verde approximately 800 meters away from the saguaro nest, with two chicks about three days old and an addled egg. This nest fledged two chicks. This trio included two banded hawks (one with an additional color band) and one

TABLE 2

Harris' Hawk Egg Productivity in Southern Arizona

	Number of nests	*Clutch size*				*Total number of eggs*	*Mean number of eggs per nest*
		1	*2*	*3*	*4*		
1969 to 1971	14	3	5	4	2	33	2.36
1972	19	0	5	8	6	58	3.05
1973	17	1	1	6	9	57	3.35
Total number of nests and eggs	50	4	11	18	17	148	2.96

with distinct plumage. In 1975 the same trio laid an initial clutch of four eggs (28 February) in an ironwood that fledged three young. On 4 June, a new nest was found with two eggs approximately 1,200 meters away from the first nest. This nest failed.

Double clutches have been observed in other North American raptors, such as the American Kestrel, *Falco sparverius* (Howell, 1932; W. R. Spofford, pers. commun.); Caracara, *Caracara cheriway* (Bent, 1937); Barn Owl, *Tyto alba* (Marti, 1968); and evidently the White-tailed Kite, *Elanus leucurus* (Pickwell, 1930). Double clutches are generally believed to be an uncommon occurrence among most raptors in the wild.

Nest Sites and Nest Success

Usually Harris' Hawks chose nest sites elevated well above the typically low desert growth of trees and bushes (Table 4). Saguaro and tree nests were about the same height. One nest in 1973 was in a red-gum eucalyptus situated almost directly over an occupied ranch house. These hawks showed great tolerance for intruders. The nest fledged one chick.

There appeared to be no definite trend to choose either saguaros or trees as nest sites from one year to the next within nesting ranges. Of 19 active nests in 1972, eleven remained intact through the next spring, and of these, four (36 percent) were used again in 1973. Harris' Hawks not uncommonly used a particular nest one year, nested elsewhere the second year, and used the first nest again the third year. I recorded this pattern four times during the study.

Bendire (in Bent, 1937) states that he found two active Harris' Hawk nests in mesquite trees and one in a cottonwood *(Populus angustifolia)* in the Tucson vicinity in 1872. In my study, none nested in cottonwoods and only one in mesquite. However, cottonwood nest sites have been reported in California (Miller, 1930), Kansas (Parmelee and Stephens, 1964), and New Mexico (Pache, 1974).

Seventy-one percent of tree nests and 59 percent of the saguaro nests were successful (Table 5). The difference is not significant ($p > .05$). Tree nests may be more successful because of the foliage that renders them less vulnerable to avian predators. On the other hand, tree nests are considerably more vulnerable to ground predators than saguaro nests. Therefore, the greatest nonhuman threat

TABLE 3

Harris' Hawk Nesting Success in Southern Arizona

	Total number of nests	*Number of successful nests*[1]	*Number of young raised to at least 28 days*	*Young per nest*
1969 to 1971	14	8 (57 percent)	17	1.21
1972	19	13 (68 percent)	33	1.74
1973	17	13 (76 percent)	30	1.76
Total number of nests and young	50	34 (68 percent)	80	1.60

[1] A nest was considered successful if a chick was raised to an age of at least 28 days. Only nests that were initially found with eggs appear in the table.

TABLE 4

Harris' Hawk Nests

Nesting sites	*Number of nests*	*Mean height (meters)*	*Range of height (meters)*
Saguaro Cactus *(Carnegiea gigantea)*	27	5.9	3.2 to 8.5
Palo Verde *(Cercidium microphyllum* or *C. floridum)*	24	5.7	4.1 to 7.3
Ironwood *(Olneya tesota)*	7	5.6	3.4 to 7.9
Mesquite *(Prosopis juliflora)*	1	5.3	0
Red-gum Eucalyptus *(Eucalyptus camaldulensis)*	1	14.9	0
Total	60	7.5	3.2 to 14.9

of predation to nests may come from avian predators, such as the Great Horned Owl *(Bubo virginianus)*.

Of the 10 Harris' Hawk nests in trees in 1972, seven (70 percent) were placed on top of a substantial growth of mistletoe *(Phoradendron californicum)*. Of the nine tree nests in 1973, seven (78 percent) were placed on such growth. This may help support the bulk of the nest or partially conceal the nest from detection by ground predators.

Mating System and Nest Success

I saw three adults at 23 (46 percent) of the 50 active nests checked (See Mader, 1976, for discussion of possible biases involved in determining a trio.). All nests were initially found with eggs. Fifty-nine percent of the nests with pairs were successful and 78 percent of the nests with trios (Table 6). The difference in nesting success is not significant ($p > .05$). Observations from blinds at three nests with trios indicated that the extra hawk served as a nest helper by either feeding the chicks and/or supplying prey at the nest. Presumably, the extra hawks at other nests also serve as nest helpers. Observations indicated that most trios remained intact through the nesting cycle. Sex ratios among nesting trios were positively determined at three nests by prior, or subsequent, trapping or, in one case, witnessing a copulation. In each instance the ratio was two males to one female.

Although I occasionally saw immatures at nests occupied by adults, I found evidence of an immature helping at only one nest. In this case the immature was a female, hatched the previous spring, that had just begun to moult into adult plumage. I visited this nest three times and on each occasion found her brooding or shading the young, or perching on the nest rim. This immature was one bird of a trio that attended the nest. The other two were adult males judging from comparative size differences.

TABLE 5

Comparative Nest Site Success of Harris' Hawks in Southern Arizona between 1969 and 1973

	Saguaro nests	*Tree nests*
Number of nests	22	28
Number of successful nests (and percentage)[1]	13 (59%)	20 (71%)
Number of young raised	34	46
Number of young per active nest	1.55	1.64

[1] A nest was considered successful if a chick was raised to an age of at least 28 days. Only nests that were initially found with eggs appear in the table.

Nesting Ranges

Harris' Hawks in southern Arizona maintain distinct nesting ranges well separated from those of conspecifics (Figure 3). A typical nesting range consists of two or three old nests, usually centered around one particular locality but, in extreme cases, may be located more than a kilometer apart from one another. In southern Arizona, a dense population averaged approximately 5.0 square kilometers per active nest. In less suitable habitat devoid of numerous saquaros and palo verde stands, a nesting range may be somewhat larger.

In 1973 Harris' Hawks occupied at least 15 (88 percent) of the 17 nesting ranges used the previous year. One pair, however, did not lay any eggs. Repeated occupancy of a nesting range by a particular Harris' Hawk occurred on some occasions. Of the 19 adults that nested in the study area in 1972, six individuals, or 32 percent, of the nesting population in 1972 were present again in the spring of 1973. Because not all of the adults were checked for bands in the study area, some banded individuals were probably missed. The number present during the second year may have been considerably higher than the computed 32 percent, possibly 50 percent or more.

Food

Mammals comprised 73.8 percent, birds 17.5 percent, and reptiles 8.7 percent of the prey remains found at Harris' Hawk nests (Table 7). Table 7 is biased because large prey items, such as rabbits, remain at nests longer than small ones. Observations from the blind (see Table 11) suggest that more birds make up the diet than Table 7 indicates. Snakes, although common in the desert, did not occur as prey items at any of the nests.

Behavior at a Polyandrous Nest

Roles of Adults

Each of the three adults at the intensively studied nest (Figure 4) filled a specific role in the nest cycle. Through approximately the first two-thirds of the observed nestling phase, the female stayed primarily in the immediate nest vicinity. In the remaining third, she sometimes ventured outside an 800-meter radius of the nest and occasionally out of sight of the blind as she searched for prey.

The female attended the nest, brooding or feeding the chicks, shading them on hot days, or simply perching nearby on a saguaro. Male 1 obtained prey and fed the chicks, and also took over the female's nest role, feeding the chicks and staying near the nest when she was temporarily absent. In contrast, Male 2 caught only prey and transferred it either to the female or to the other male. The amount of time spent on the nest and in the nest tree by the individual adults is shown in Table 8.

Vocalizations

I recorded four different calls by Harris' Hawks plus slight variations of each. One call, the Begging Call, was given only by chicks or first year birds. This call is perhaps best described as a plaintive scream resembling the sound *eechip* and lasting approximately two seconds. The Chirp Call, usually given by an adult anticipating a prey exchange or food delivery, was an *eerrp* sound lasting from one to three seconds. A third vocalization, the Alarm Call, was given commonly when a human observer or large animal entered a nesting area. It resembles the sound *iirr* and lasts approximately three seconds. The last call, a Cackle Call, seldom given, resembles somewhat a Cooper's Hawk's (*Accipiter cooperii*) cackle but sounds like a quick succession of four or five chirps given at one-second intervals for five to ten seconds. Male 2 gave this call when he had prey and the female refused to receive it because she, too, had prey. In the other cases, single adults rendered the call after I had intruded into their nesting territory.

TABLE 6

Comparative Nest Success of Harris' Hawk Pairs and Trios

	Pairs	*Trios*
Number of nests	27	23
Number of successful nests (and percentage)[1]	16 (59%)	18 (78%)
Number of young raised to at least 28 days	35	45
Number of young per nest attempt	1.30	1.96
Number of young per successful nest	2.19	2.50
Number of young per nesting adult[2]	0.73	0.65

[1] A nest was considered successful if a young bird was raised to an age of at least 28 days. Only nests that were initially found with eggs appear in the table.

[2] Figure for pairs includes three renestings; total number of adults = 48.

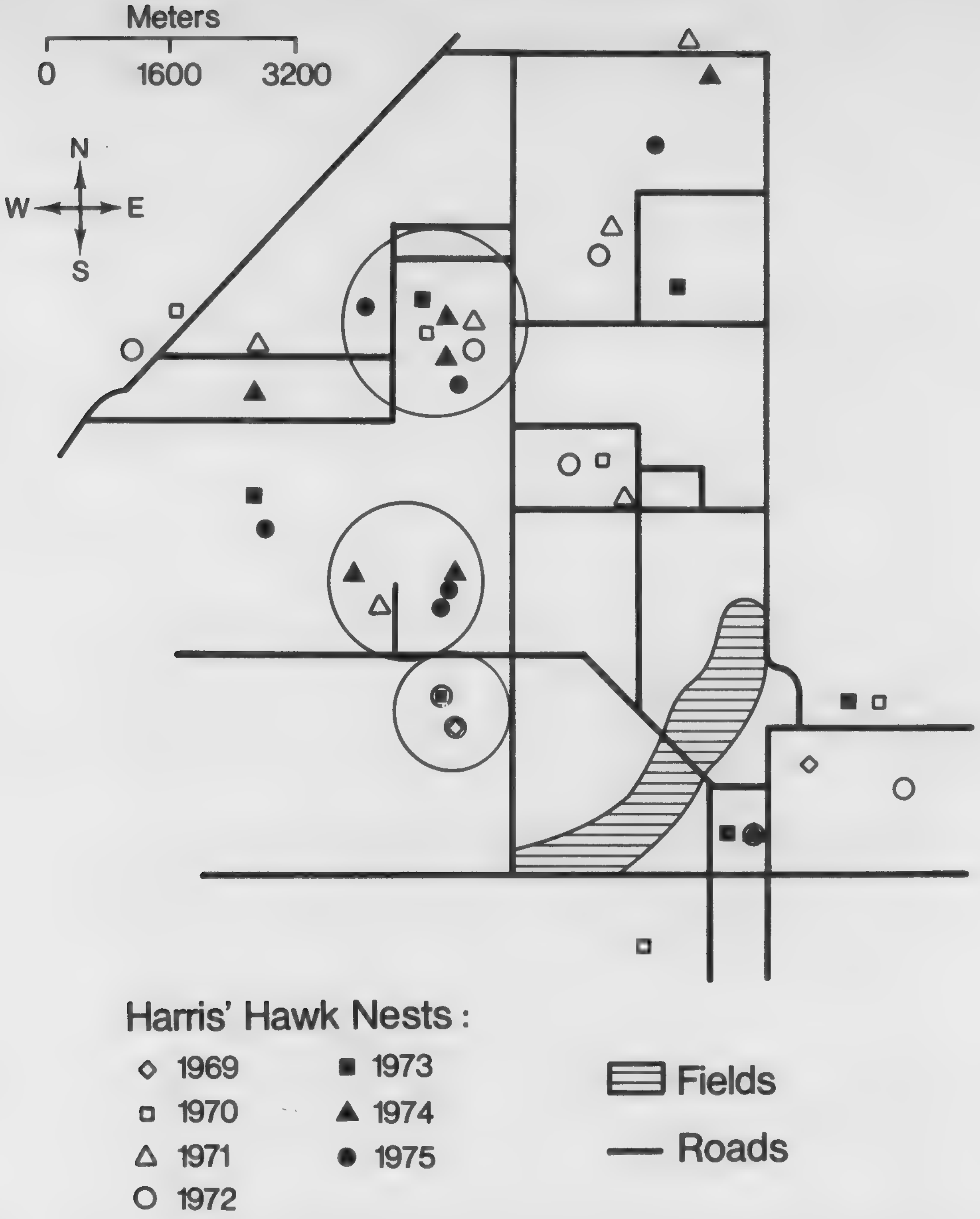

Figure 3. Map showing active nests of Harris' Hawks in the desert study area 38 square kilometers in size in Pima County, Arizona. Map includes nests found from 1969 to 1975. All initial nests with eggs were located from 1971 to 1975. Some second nesting attempts may have been missed. Circles with two symbols of the same kind represent second nesting attempts for the respective year; in three of the five cases, both nests were successful.

Feeding

The nestlings received most of their food from the female (Table 9; Figure 5). However, during the third week of observation Male 1 fed the young nearly twice as much as did the female. The increased feeding by this male paralleled the period of rapid growth in the late nestling stage when the need for food was greatest. Generally, if the female arrived at the nest while Male 1 was feeding the young, the male either passed the prey item to the female with his bill or stepped off the prey and left the nest. On one occasion, I observed both the female and Male 1 feeding the young simultaneously with separate food items. I witnessed the same feeding behavior at both of the nests studied in 1972. Male 2 did not feed the nestlings or associate closely with them.

TABLE 7

Prey Remains Found at Harris' Hawk Nests in Southern Arizona

Species	*Number of items*	*Percentage of total*
Mammals:		
Harris ground squirrel, *Citellus harrisii*	20	12.5
Round-tailed ground squirrel, *C. tereticaudus*	3	1.9
Wood rat, *Neotoma lepida*	20	12.5
Cottontail rabbit, *Sylvilagus audubonii*	67	41.9
Black-tailed jack rabbit, *Lepus californicus*	3	1.9
Unidentified mice	1	0.6
Unidentified rabbits or hares	4	2.5
Total Mammals	118	73.8
Birds:		
Gambel's Quail, *Lophortyx gambelii*	8	5.0
Cactus Wren, *Campylorhynchus brunneicapillus*	4	2.5
Mourning Dove, *Zenaidura macroura*	2	1.3
Bendire's Thrasher, *Toxostoma bendirei*	1	0.6
Roadrunner, *Geococcyx californianus*	1	0.6
Gilded Flicker, *Colaptes chrysoides*	1	0.6
Unidentified thrashers, *Toxostoma* sp.	7	4.4
Unidentified birds	4	2.5
Total Birds	28	17.5
Reptiles:		
Desert spiny lizard, *Sceloporus magister*	9	5.6
Zebra-tailed lizard, *Callisaurus draconoides*	1	0.6
Unidentified lizards	4	2.5
Total Reptiles	14	8.7
Total number of prey remains	160	100.0

Delivery of headless prey to the nest by the adults diminished as the young grew. When a whole prey item was brought to the nest, the adults often began feeding at the head. Partially consumed items were sometimes left on the nest for later feedings.

Adults generally carried the remains of prey from the nest in the bill or, if large, in the feet. Of 25 observed instances, adults transferred 22 prey items (88 percent) from the bill to the feet while 5 to 12 meters from the nest. Intestines of prey were fed to the young, eaten by the adults, or carried from the nest to a tree or saguaro and discarded.

Nest Activity

The adult female and Male 1 had set patterns for approaching the nest. Of 94 landings in the nest tree which I witnessed in 1973, the female landed on a patch of mistletoe one meter above the nest 83 percent of the time or landed directly on the nest 17 percent of the time. Male 1 also landed on the mistletoe or the nest, but with exactly the opposite frequency (17 and 83 percent, respectively).

Shading of the young by the female occurred infrequently. I saw it four times in 1973 and it lasted from 1 to 38 minutes (mean = 16). The female oriented her back to the sun and allowed her shadow to fall over the nestlings. Sometimes she drooped her wings. The nestlings appeared to be able to tolerate extreme heat and direct sunlight.

The female sometimes excavated into the nest by stooping down and rearranging debris in the nest cup with her bill. This was done by pushing, pulling, and side-to-side movements of the head. These Bill-dig activities are well pronounced in Goshawks *(Accipiter gentilis)*, and Schnell (1958) postulated that such activity is probably influenced by the estrogen level of the female. Ellis (1973:99) proposed three functions of Bill-dig in the Golden Eagle *(Aquila chrysaetos)*. During the incubation period, the adults Bill-dig in the nest cup, and thereby bring fine litter to the surface where it serves to more efficiently insulate the eggs. Eagles also Bill-dig to clean the bill after feeding and to locate, pursue, and remove arthropods that inhabit the nest matrix.

Back Standing

Sometimes, one of the males alighted on the back of the female and quietly stood there from 3 to 90 seconds (Table 10). No hostility was apparent during these interactions and all occurred on saguaros. It appeared that some back-standing was the result of one hawk wanting the perch of another. In these cases the hawk on the bottom seemed to grow tired of supporting the other hawk and flew, leaving the hawk on top with the perch. On occasions when the bottom hawk had prey, the bird on top may have been anticipating a prey exchange.

Hunting

I observed all three adult Harris' Hawks hunting prey in the nest vicinity at all times of the day. The males did most of the hunting. The female began hunting occasionally in the last 18 days of the observation period. Prey that I observed brought into the nest or nest vicinity (Table 11) consisted of mammals (57.1 percent), birds (35.2 percent), and reptiles (7.7 percent). In 1973 I determined which adult caught the prey. Of the 52 prey captures in which I identified the adult, 25 prey captures (48 percent) were by Male 1, 18 (35 percent) by Male 2, and nine (17 percent) by the female. Comparing only prey caught by the two males, Male 1 brought in 58 percent of the prey and Male 2, 42 percent. All adults caught similar kinds and sizes of prey.

In 14 instances, I determined when a prey item had been caught. This was done either by having watched a successful hunting attempt or having seen a hawk just arrive on top of a saguaro with prey that was still alive. Average time from capture of prey to delivery of prey at the nest was 39 minutes and ranged from two minutes to three hours and 25 minutes. Because of the partially eaten state of some of the prey items brought to the nest, I could not determine what percentage consisted of fledgling birds and young mammals.

I witnessed 61 instances of attempted prey capture, of which 10 (16 percent) were successful (Table 12). Adult Harris' Hawks commonly hunted prey in groups in what appeared to be a cooperative effort. On seven (11 percent) of the 61 capture attempts, both males cooperated. Rudebeck (*in* Brown and Amadon, 1968) found Peregrine Falcons *(Falco peregrinus)* and Merlins *(Falco columbarius)* on migration to have 7.5 and 5.0 percent success, respectively, in hunting. Of 469 prey attempts by Ospreys *(Pandion haliaetus)* in Nova Scotia, 419 (almost 90 percent) were successful (Brown and Amadon, 1968). The degree of hunting success is probably attributable to the species hunting, prey species and abundance, habitat, and weather conditions.

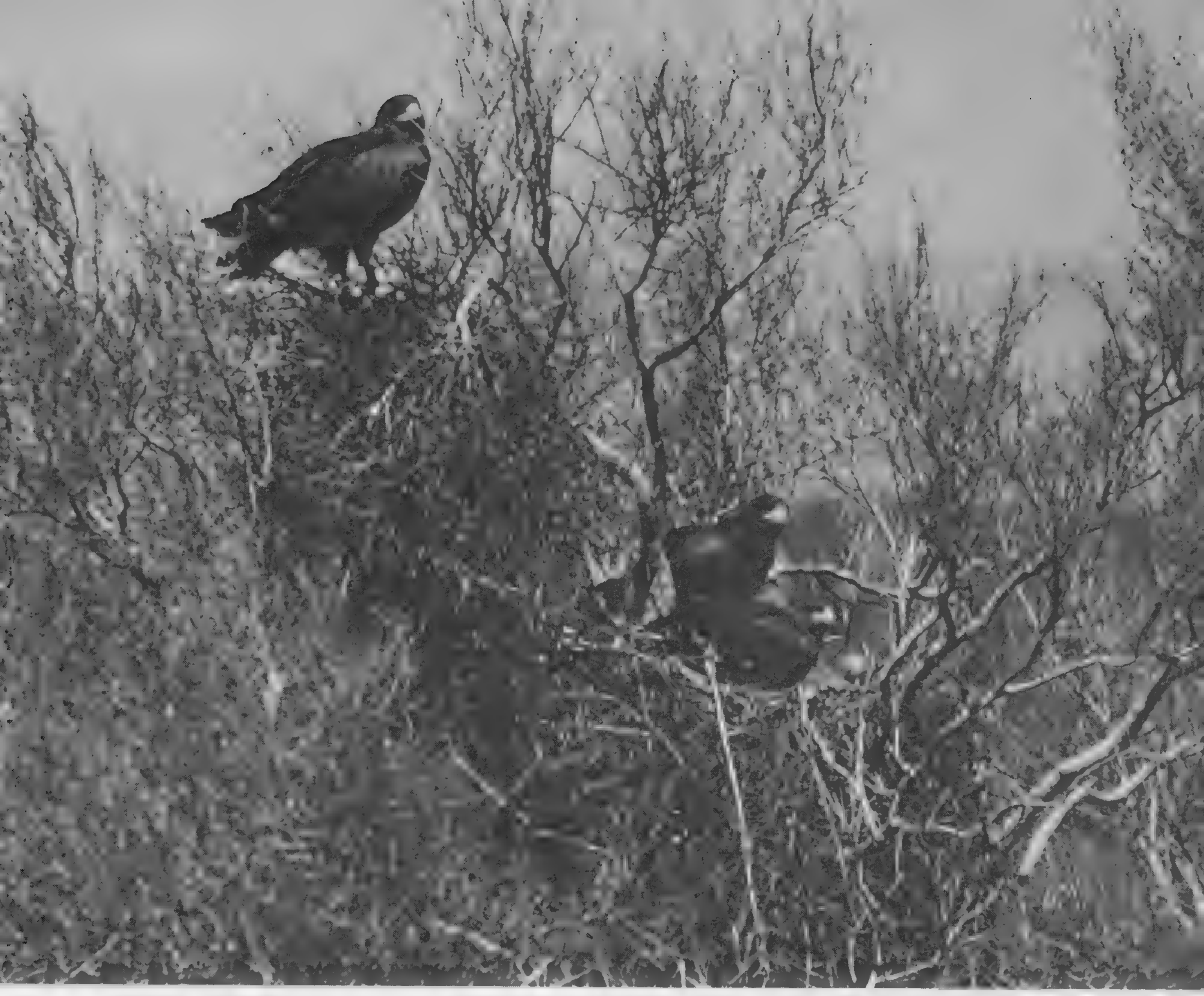

Figure 4. The female, Male 1, and Male 2 at the intensively studied nest of Harris' Hawk in 1973.

In the initial stoop to capture prey, an adult Harris' Hawk either descended in a quick glide from a tree, saguaro, or soaring position with limited wing-flapping, or it flew out horizontally from a perch and remained at a fixed altitude until it plunged steeply downward. If the initial attempt was successful, the hawk remained on the ground with the prey for a few seconds, or flew immediately to a nearby elevated perch to feed. If unsuccessful, the hawk sometimes took a perch close to the last sighting of the prey and remained there until the prey reappeared, or until the hawk tired of waiting and flew back to a saguaro or tree. If the prey flushed, the hawk went after it with quick wing beats. When the flushed prey was chased into cover, the hawk sometimes swooped vertically upwards about one to eight meters, made a tight circle, and then descended on the prey if it reappeared. In some cases the hawk simply stooped to secure the prey without circling. On the other hand, some Harris' Hawks occasionally end the chase with the first miss, fly to a perch, and begin the hunting process all over again. I did not observe hovering Harris' Hawks in hunting attempts. Hunting methods suggested that most of the birds caught were secured on the ground or in brush and probably not in level flight. When two or three hawks participated in hunting, they either went after the prey at the same time or took turns chasing it.

The two adult males at the nest under concentrated study appeared to hunt at maximum capacity throughout the observation period, even though the need

TABLE 8

Nest Attention by Three Adult Harris' Hawks at an Observation Nest

	Ages of young in days					
	1-7	*8-14*	*15-21*	*22-28*	*29-35*	*36-42*
Total period of observation[1]	33:25	22:40	32:20	20:40	22:30	26:05
Total time female was on nest	12:31	05:47	03:31	01:48	00:35	00:27
Female's brooding time expressed as a percentage of her total time on nest	57	22	00	00	00	00
Total time Male 1 was on nest	00:14	00:38	03:03	00:11	00:06	00:18
Total time Male 2 was on nest	00:03	00:00	00:00	00:00	00:00	00:00
Total time the nest was attended by an adult (expressed as a percentage of the observation time)	38	28	20	10	03	03
Total time female perched in nest tree	00:18	00:30	00:20	00:23	00:18	00:05
Total time Male 1 perched in nest tree	00:00	00:00	00:01	00:00	00:00	00:00
Total time Male 2 perched in nest tree	00:01	00:00	00:00	00:00	00:00	00:00
Total time an adult perched in nest tree (expressed as a percentage of the observation time)	01	02	01	02	01	00

[1] Times expressed as hours and minutes.

for food at the nest did not always seem to require it. In a feeding-rate experiment conducted at two Cooper's Hawk nests in Arizona, the results suggested that the hawks hunted at maximum even though the brood size varied from two to five chicks (Snyder and Snyder, 1973). A similar situation may exist in Harris' Hawks, whereby the adults do not adjust their hunting in terms of the need to supply food at the nest. This means that each pair or trio puts forth its maximum reproductive effort every spring regardless of low or high prey densities. If maximum hunting capacities exist in Harris' trios, this may be an adaptation assuring nest success in low prey years, even though maximum hunting persists in high prey years when the need is not as great. I have discussed elsewhere (Mader, 1976) why trios may be more successful than pairs.

Prey Exchanges

I witnessed 46 prey exchanges between adult Harris' Hawks at or near the intensively studied nest in 1973 (Table 13); all occurred within 150 meters of the nest. Twelve exchanges took place at the nest itself. Prey exchanges usually took place at favored saguaros or trees in the nest vicinity. However, in 1974, five prey exchanges took place at two old nests in an ironwood and saguaro, 35 and 158 meters, respectively, from the active nest. One of the two

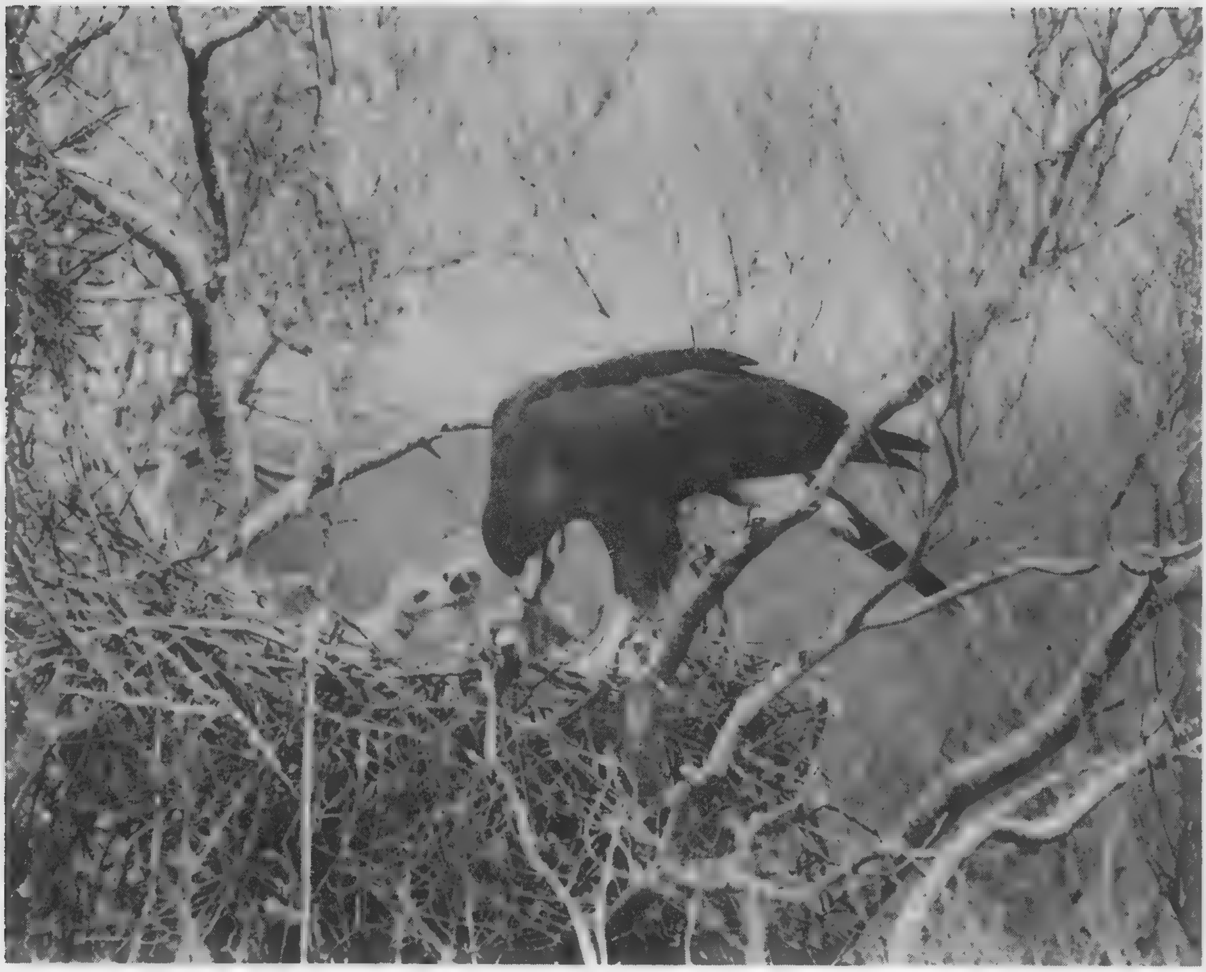

Figure 5. Adult Harris' Hawk feeding young.

TABLE 9

Feeding Attention by Two Adult Harris' Hawks at an Observation Nest

	Ages of young in days					
	1-7	*8-14*	*15-21*	*22-28*	*29-35*	*36-42*
Total period of observation[1]	33:25	22:40	32:20	20:40	22:30	26:05
Female's feeding time	03:42	01:25	01:24	00:46	00:12	00:04
Male's feeding time	00:00	00:29	02:40	00:03	00:02	00:01
Total feeding time	03:42	01:54	04:04	00:49	00:14	00:05
Average feeding time per feeding visit	00:12	00:09	00:14	00:07	00:05	00:02
Total feeding time expressed as a percentage of the total time on the nest by an adult	29	30	62	41	34	11
Total feeding time expressed as a percentage of the observation time	11	08	13	04	01	00

[1] Times expressed as hours and minutes.

TABLE 10

Number of Times an Adult Harris' Hawk Stood on Top of Another at Two Nests

	Male 1 on female	*Male 2 on female*	*Male 2 on Male 1*	*Male 1 on Male 2*
Total times observed	11	11	7	1
Mean in seconds	18	18	9	8
Range in seconds	3 to 90	5 to 53	3 to 28	0
Number times hawk stood upon had prey (and percentage)	4 (36%)	4 (36%)	1 (14%)	0

prey exchanges that took place on the ground in 1973 occurred when the female accidentally dropped the prey from a saguaro. The number of calls given by adults prior to a prey exchange varied considerably. In some cases no calls were given, while in one instance Male 2 gave 41 chirps and the female 140 chirps within a 15-minute period prior to receiving prey from the male. Even after an exchange of prey, an occasional chirp or alarm call might be given by one or both birds. Male 2, when approached by Male 1, sometimes refused to give the prey to Male 1. In comparison, Male 2 always passed prey to the female. Most prey exchanges were harmonious, with no hostile behavior exhibited on the part of the participants.

Male 2 gave three prey items to a four-month-old Harris' Hawk with a broken wing (1974), while the trio still had nestlings from the second brood. This immature was from a previous brood that the trio had raised earlier that year. The immature received all its prey from Male 2 on the ground, 42 to 140 meters from the nest. This hawk was found dead 13 meters from the nest shortly afterward. Cause of death was not known.

A prey item was exchanged among all three adults on five occasions in 1973 and 1974. Only in three cases was it finally brought to the nest. I observed a three-way exchange of prey twice at a nest in 1972.

Caching of uneaten portions of prey appeared to occur infrequently. I saw it only twice (1973 nest). The female cached a lizard, and an unidentified adult cached a quail. Intense desert heat, possibly spoiling the prey, may be the cause of so little caching behavior by nesting Harris' Hawks.

Nesting Range Intrusions

Harris' Hawks are decidedly more tolerant of most raptor intruders when compared with other hawks. I observed 14 instances of intrusion by alien hawks into the nesting range of the trio under intensive study in 1973. An immature Harris' Hawk, presumably the same bird, made ten of these boundary violations. Reactions of the adults varied from playfulness to aggressiveness toward the trespassing immature, which generally was not allowed to get close to the nest. If the intruding immature flew within 30 meters of the nest, one, two, or all three adults quickly chased it away; but they tolerated the immature if it soared about 60 meters or more over the nest. In many instances the immature participated in playful attacks against the adults and vice versa. Usually, when the trespassing hawk entered the nesting range, one of the three occupants gave a chirp or defense call before hostilities began.

On two other occasions, nonresident adult Harris' Hawks entered the trio's territory. One instance involved an adult circling over the nest. In the other, two adults from another nesting range approximately 1,400 meters away flew into the area and soared with Male 1 and 2 over the nest at an altitude of about 120 meters. On both of these occasions, no agonistic behavior occurred. In another intrusion, a Red-tailed Hawk soared with Males 1 and 2 over the nest site. At another nest, an adult Harris' Hawk dived at a Great Horned Owl I had flushed off a nest. Except for this case, I found Harris' Hawks nesting in relatively close proximity (about 180 meters) to Great Horned Owls without observed hostilities. Freemyer and Freemyer (1970) found nests of these two species in Texas only 27 meters apart. In this case, however, the two adult hawks dived at the incubating owl when it was on the nest and flying to and from it.

Galapagos Hawks, although commonly nesting in trios, furiously fight with neighboring pairs to defend territories (de Vries, 1973).

In response to stray dogs or coyotes passing near the intensively studied nest, adult Harris' Hawks gave an alarm call. Sometimes after this initial response, the hawks circled the animals at about 30 meters and "escorted" them away from the nest area.

A human observer received much the same response as an intruding dog or coyote. When I walked to the blind, the adults rendered alarm calls 89 per-

TABLE 11

Prey Items Observed Brought to Two Harris' Hawk Nests and Nest Vicinity in Two Successive Years (1973 and 1974) by Three Adult Harris' Hawks

Species	*Number of items*	*Percentage of total*	*Percentage of total biomass*
Mammals:			
Harris ground squirrel, *Citellus harrisii*	15	16.4	10.5
Round-tailed ground squirrel, *C. tereticaudus*	9	9.9	7.7
Wood rat, *Neotoma lepida*	11	12.1	11.2
Kangaroo rat, *Dipodomys merriami*	1	1.1	3.0
Cottontail rabbit, *Sylvilagus audubonii*	9	9.9	38.9
Unidentified rats or mice	7	7.7	0.8
Total Mammals	52	57.1	72.1
Birds:			
Gambel's Quail, *Lophortyx gambelii*	17	18.7	18.5
Cactus Wren, *Campylorhynchus brunneicapillus*	1	1.1	0.2
Mourning Dove, *Zenaidura macroura*	1	1.1	0.8
Curve-billed Thrasher, *Toxostoma curvirostre*	3	3.3	1.6
House Finch, *Carpodacus mexicanus*	1	1.1	0.1
Unidentified birds	9	9.9	5.0
Total Birds	32	35.2	26.2
Reptiles:			
Desert spiny lizard, *Sceloporus magister*	2	2.2	0.8
Western whiptail lizard, *Cnemidophorus tigris*	3	3.3	0.4
Unidentified lizards	2	2.2	0.5
Total Reptiles	7	7.7	1.7
Total number of prey items	91	100.0	100.0

cent of the time during the first two-thirds of the observation period and 50 percent the last third. The reduction in vocal response can be attributed to a more relaxed defense of the growing chicks and the increased absence of the adults when hunting pressures are great.

Alarm calls and circling by the adult hawks above a nest seemed to attract other adults and immatures. In one exceptional case, I approached a nest and discovered seven Harris' Hawks circling overhead. The four hawks, in addition to the trio at this particular nest, probably came from neighboring nesting ranges.

At the nest under intensive study, I did not witness hiding reactions in which the hawks flatten themselves into the nest depression at the approach of a human. I did observe this intruder reaction, however, at several other nests. It is widespread in falconiforms.

Nestling Development

The nearly constant attention focused on the activities of the adults at the nest under intensive study permitted only limited observations of the nestlings (Figure 6). For this reason, only some aspects of the young's development will be discussed.

A light brown down covers the newly hatched nestlings. In nine to 13 days this down nearly disappears and gray down emerges. At this time the dorsal tract is evident and primaries emerge. Weight increases of Harris' Hawk nestlings are plotted in Figure 7.

From the first day onward at the nest, the young gave begging calls. One-day-old nestlings gave low intensity begging calls that consisted of short, high-pitched chirps. At the age of 15 days, the young gave begging calls upon seeing the adults fly overhead. They picked at prey items in the feet of an adult when they were 17 days old. At this stage they also picked up pieces of meat that had been dropped in the nest. Previously, only an adult feeding the young picked up and ate these leftovers. At 18 days of age the young could feed themselves, although I recorded adults feeding young up to 40 days of age. Nestlings perched in branches near the nest at approximately 40 days. Eye color in immature Harris' Hawks gradually changes from a dark brown to a light brown by the time the hawks attain adult plumage in their second year.

TABLE 12

Attempts to Capture Prey by Three
Adult Harris' Hawks Near Two Nests in 1973 and 1974

	Number of participating adults in each attempt			
	1	*2*	*3*	*Total*
Number of attempts (and percentage of attempts by all three adults)	32 (52%)	17 (28%)	12 (20%)	61
Number of successful attempts	5	3	2	10
Number of successful attempts expressed as a percentage of the total number of capture attempts	16	18	17	16

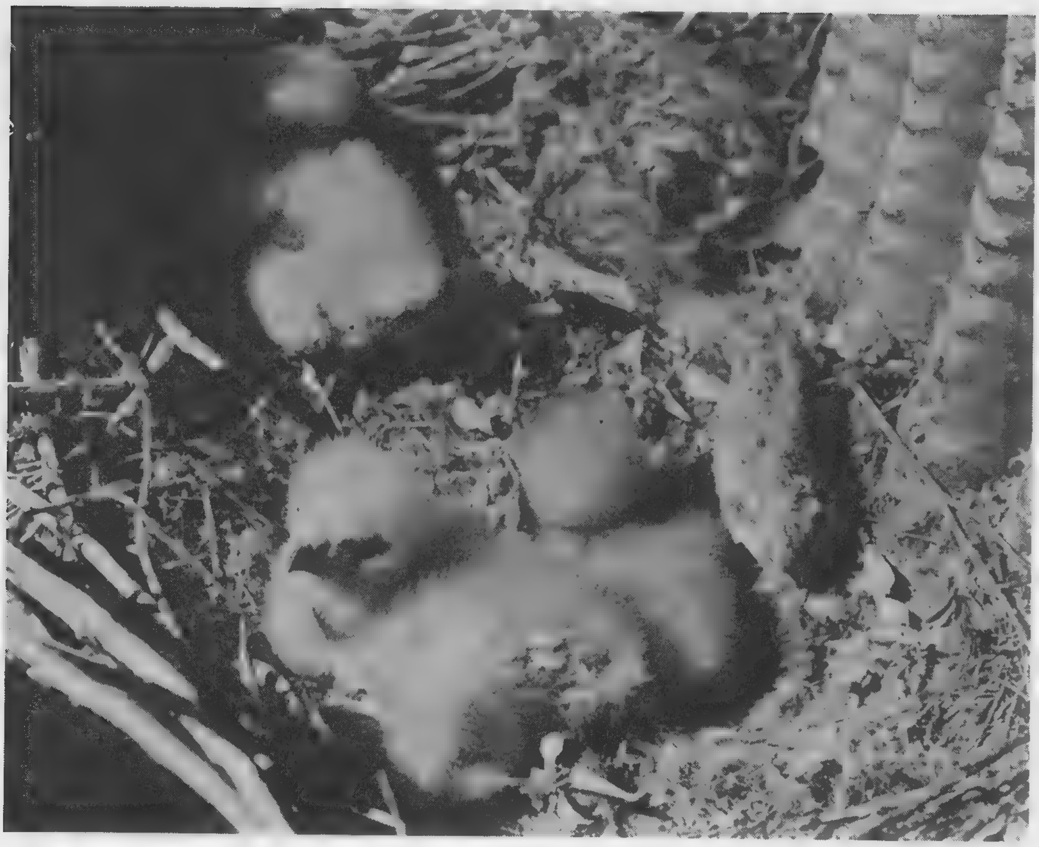

Figure 6. Three young Harris' Hawks in a saguaro nest.

TABLE 13

Prey Exchanges Between Three Adult Harris' Hawks at a Nest and Nearby Vicinity

	Male 1 to female	*Male 2 to female*	*Female to Male 1*	*Male 2 to Male 1*	*Male 1 to Male 2*	*Female to Male 2*
Number of exchanges	22	13	4	4	2	1
Mean distance from nest (meters)	135	113	112	129	115	116
Exchanges with chirps given by both hawks	0	1	0	0	1	0
Exchanges with chirps given by one hawk	4	5	0	1	0	1
Exchanges at nest	11	1	0	0	0	0
Exchanges on saguaros	7	4	2	3	1	1
Exchanges in trees other than nest tree	2	5	0	1	1	0
Exchanges on ground	0	0	2	0	0	0
Exchange site unknown	2	3	0	0	0	0

At all the nests I observed from blinds, I recorded little aggression among the nestlings when one had food. In Goshawks (Mader, pers. observ.; Schnell, 1958; Snyder and Snyder, pers. commun.), Cooper's Hawks, and Sharp-shinned Hawks, *Accipiter striatus* (Mader, pers. observ.; Snyder and Snyder, pers. commun.), young birds vigorously defended their food when they were old enough to feed themselves. They protected food from nest mates by screaming or covering the food from view with their wings. The non-feeding young usually responded to such behavior by taking a position on the rim of the nest facing away from the feeding young, sometimes bending over slightly. Snyder and Snyder (pers. commun.) postulate that such a position indicates a passive, non-aggressive attitude by the non-feeding young and helps prevent attack by the nestling with food.

This lack of feeding hostility among Harris' Hawk nestlings may be a conditioner whereby family groups may cooperate in hunting, and possibly feeding, at a later date. I have witnessed some possessive hostility among adults over prey, but it is decidedly of low intensity when compared with other raptors. I also recorded mimicking of one nestling's actions by another. If one nestling flapped its wings and jumped to a nearby branch, one or more nest mates sometimes followed.

Immature Harris' Hawks usually stayed in the nest vicinity for at least two to three months after fledging. The three color banded immatures at the intensively studied nest were still present within 1,200 meters of the nest 81 days after they fledged.

Young Harris' Hawks several days old. Drawing by Tony Angell.

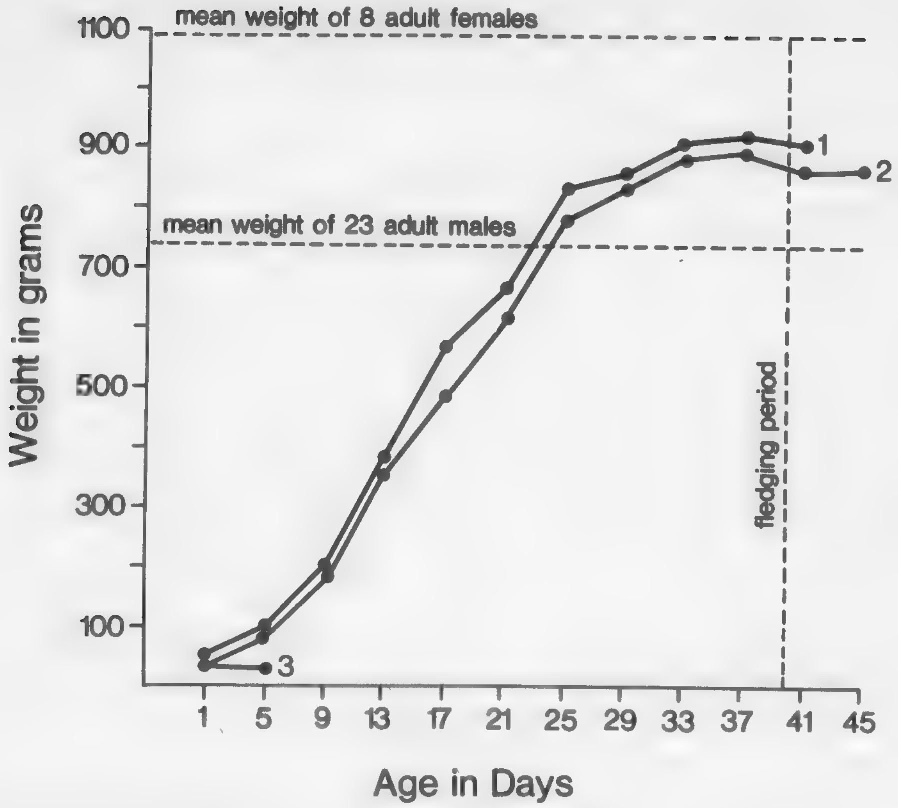

Figure 7. Weight increases of young Harris' Hawks measured once every four days. The three development curves are for two young females (1 and 2) and an immature (3) that died after five days of age.

Conclusion

Observations indicate that the Harris' Hawk is, so far as known, a behaviorally unique falconiform. Nest helpers in this species may be common in Arizona. The Galapagos Hawk, an endemic island species (de Vries, 1973), is the only other falconiform known to engage commonly in nest-helping roles. Nest helpers, undefended nesting ranges, group prey exchanges at nests, polyandrous copulation, family groups in winter, and the general lack of intraspecific aggression in the Harris' Hawk suggest that group or family relationships are an important aspect of this species' biology. It is not entirely clear why such a social organization evolved. Possible advantages of trios over pairs in the Harris' Hawk are discussed in another paper (Mader, 1976). Briefly, an extra adult (1) could probably increase prey supplies at a nest thereby insuring greater fledgling success in low prey years, (2) would leave more time for the primary nest-attending hawk to guard the nest from predators, and (3) if one adult perished, the other two could probably shift their parental roles and avoid loss of the brood.

Harris' Hawk populations in southern Arizona appear to be concentrated in certain localities and totally absent in others. This is probably the result of the distribution of saguaro-palo verde flatland, indispensable to Harris' Hawk survival in the desert. To my knowledge there are three large populations of Harris' Hawks in southern Arizona, with small isolated groups nesting in between. The dense Harris' Hawk population in the study area is now declining from habitat destruction and will have largely disappeared within 10 years. Once the saguaro-palo verde habitat vanishes, it is doubtful if Harris' Hawks in southern Arizona could shift and survive in a marginal habitat devoid of saguaros and palo verdes. If this happens, it may be only a matter of decades before all but a few remnant Harris' Hawk groups have disappeared.

Summary

An intensive study was conducted on the Harris' Hawk populations in Pima and Pinal Counties, Arizona from 1971 to 1973. Incidental investigations on Harris' Hawks were made from 1969 to 1975. Harris' Hawk populations in southern Arizona are largely non-migratory and appear to be strictly correlated with saguaro-palo verde type habitat in the flatlands of the Lower Sonoran Desert.

Excluding recaptured nestlings, I trapped and banded 42 Harris' Hawks during the winters (31 males, 11 females; 2.8 males per 1.0 female). Females were about one-third larger than males in weight with no overlap in wing and weight measurements. I sexed 107 Harris' Hawk nestlings (56 males, 51 females; 1.1 males per 1.0 female). Car censuses and banding data indicated that this species formed groups for indefinite periods of time in the winter. Groups sometimes included one or two families totaling three to six hawks.

The incubation period for six clutches averaged 35 days. Fifty clutches averaged 2.96 eggs and yielded 1.60 chicks per active nest. Harris' Hawks not only nested in adult pairs but also groups of three adults (trios). Of 50 nests, 27 (54 percent) were pairs and 23 (46 percent) trios. Nests with trios were 19 percent more successful than those with pairs.

I observed Harris' Hawks nesting in saguaro cacti, palo verde trees, ironwood trees, a mesquite, and a red-gum eucalyptus tree. Tree nests were 12 percent more successful than saguaro nests.

An intensive study of a Harris' Hawk trio (two males and one female) showed that each adult had well defined roles in the nesting cycle. Two and sometimes all three adults commonly cooperated in catching prey. Of 91 observed prey deliveries at two nest sites used by these birds in successive years, 57.1 percent were mammals, 35.2 percent birds, and 7.7 percent reptiles. Of 160 prey remains found at various nests, 73.8 percent were mammals, 17.5 percent birds, and 8.7 percent reptiles. Snakes, although common in the desert, did not occur as prey items at any of the nests.

Harris' Hawks did not nest communally but maintained distinct nesting ranges that were not defended from other adults of the species. At five nests, two successive clutches of eggs were laid either in the same nest (once) or in a newly built or repaired one (four times). In all cases but one, the initial and second clutches were successful and raised at least one young. In the one case, the first clutch produced three young and the second failed.

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Red-tailed Hawk, *Buteo jamaicensis.* Drawing by Ted Lewin.

FACTORS INFLUENCING FEMALE CHOICE IN THE LEK MATING SYSTEM OF THE RUFF

Julia M. Shepard

The natural history of the Ruff, *Philomachus pugnax,* was documented by Witherby *et al.*, (1952). This medium-sized inland wader of the family Scolopacidae breeds across northern Europe and Asia. Marked sexual dimorphism of breeding plumage characterizes the Ruff. To a lesser degree, this sexual distinction extends to body size as well, the males being somewhat larger. Hogan-Warburg (1966) described the morphological features of the Ruff in detail. Male Ruffs develop an elaborate nuptial plumage consisting of a large, erectile, pectoral ruff, two erectile head tufts, long ornamental feathers on the back, and small colored wattles on the bare skin of the face. The male nuptial plumage shows extreme individual variation of color and pattern (Hogan-Warburg, 1966), resulting in striking color polymorphism. The female nuptial plumage is a brighter, more conspicuously patterned version of the drab and cryptic non-breeding plumage of both sexes.

Social System

The Ruff has a promiscuous "lek" mating system. A lek is a traditional, collective (Hjorth, 1970) display ground composed of grouped display territories, each of which is defended by a different male. Males gather on leks for display during the breeding season. Females visit leks for copulation with males. The display territories serve as copulation sites. No pair-bond is formed between males and females. Males on a lek compete for the attraction of females and the opportunity to copulate. Feeding and nesting occur off the lek. Females nest solitarily and receive no help with nesting duties from the emancipated males. Males continue to display on the leks throughout most of the breeding season.

A Ruff lek is a complex community. The excellent definitive study conducted by Hogan-Warburg (1966) described the social behavior of Ruffs on the lek, and discovered the existence of an unusual diethism (meaning two behaviors, i.e., two behavioral types of males) among male Ruffs. This phenomenon was termed "behavioral polymorphism" by Hogan-Warburg (1966) and "behavioral dimorphism" by van Rhijn (1973). The term "diethism" (William C. Dilger, pers. commun.) seems more precise, and therefore it is substituted here.

Within the male society, two types of males coexist that are characterized by differences in behavior. Also, incompletely understood differences in nuptial plumage coloration are associated with the behavioral differences. The two male types are called (1) independent males and (2) satellite males. Independent males perform aggressive behaviors that enable them to acquire and maintain display territories on a lek. These males may be differentiated further as being resident, or the actual owners of display territories, and marginal, which are either potential owners of display territories, or owners at neighboring leks. Independent males typically have colored or dark nuptial plumage (Hogan-Warburg, 1966, Table 13). Satellite males perform predominantly non-aggressive behaviors during the breeding season, and are non-territorial. Rather than owning a display territory, a satellite male makes use of display territories of tolerant resident males. The satellite male temporarily stays together with a resident male, jointly occupying the display territory with the host. A satellite male freely changes hosts within a lek and visits different leks. Satellite males typically have white or light nuptial plumage (Hogan-Warburg, 1966, Table 13).

Females visit leks for copulation with males. The female indicates her "choice" of partner for copulation by selecting a male's display territory at which she solicits for copulation by crouching low to the ground with the tail held higher than the head. Female preference for particular display territories, and the gradual shift of this preference from one display territory to another during the course of a breeding season, have been reported by Selous (1906-1907), Bancke and Meesenburg (1958), and Hogan-Warburg (1966). Possible factors influencing female preference in Ruffs have been proposed by Selous (1906-1907), Hogan-Warburg (1966), and van Rhijn (1973). However, the factors that direct the females' choice of partners for copulation are still relatively unknown. This paper presents an investigation into the mechanisms of female choice in the lek mating system of the Ruff, and contributes a beginning quantitative analysis of data in relation to previously proposed hypotheses concerning female choice.

Methods

Study Area

I made the observations reported in this paper on the Baltic Sea island of Öland, Sweden at 56° 15′ N Lat. and 16° 30′ E Long. Two small leks containing four to eight resident males were studied in the vicinity of the village of Ottenby, on an extensive, wet grassy moor at the southeastern end of the island. One lek, hereafter referred to as SP Lek, was situated in an area of grassy hummocks near a large pond. Directly north of SP Lek stretched a broad, shallow flooded depression that provided a feeding ground closeby for the Ruffs. Another lek, referred to as TP Lek throughout the article, was located approximately one mile north of SP Lek on the same moor. TP Lek was established on a slightly elevated, short-grass ridge between a pond to the west and a shallow flooded trough to the east, both of which provided nearby feeding grounds for the Ruffs.

Procedures

I conducted field work on breeding Ruffs during the months of April, May, and June in 1970, 1971, and 1972. The quantitative data presented in this paper were collected during periods of intensive observation from 2 to 15 May, 1971, and 1 to 16 May, 1972. Observations were made during the early morning hours, beginning just before sunrise when the males arrived, from 03:00 to 04:00, and ending when lek activity declined from 08:00 to 10:00 (Table 1). In 1971, I collected quantitative data only at SP Lek, while in 1972, I gathered quantitative data at both SP and TP Leks.

A 20X spotting scope placed approximately 20 meters from the lek was used for observing the Ruffs. In 1971, I made observations from a one-meter-cube blind; but in 1972, because extremely strong winds prevented the use of a blind, I recorded data without a blind. I documented resident and satellite males on film using a 35mm camera and 300mm telephoto lens. Observations were verbally recorded into a cassette tape recorder.

I did not band or mark the Ruffs in any way, due to the difficulty of catching them and to a desire not to disturb the lek. Nonetheless, all resident and satellite males on both leks were individually recognizable by their distinctive nuptial plumages.

TABLE 1

Observation Periods at Leks

Date	*Time*	*Date*	*Time*
SP Lek 1971			
2 May - 15 May	04:00-08:00		
SP Lek 1972		TP Lek 1972	
1 May	04:00-10:00	5 May	10:00-10:30
2 May	04:00-08:00	6 May	05:25-06:45
3 May	04:00-07:30		10:00-10:30
4 May	04:00-07:00	7 May	04:00-07:00
5 May	04:00-07:00	8 May	04:00-07:00
6 May	04:00-05:00	9 May	04:00-06:00
	09:00-09:45	10 May	04:00-06:45
9 May	06:20-07:15	14 May	04:00-06:45
11 May	04:00-06:30	15 May	04:00-07:00
12 May	04:00-07:00	16 May	04:00-06:45
13 May	04:00-07:00		

Description of Male Nuptial Plumages

A standardized method was developed for describing nuptial plumages of individual male Ruffs. The method used the distinctive colors and patterns of the head tufts and neck ruff. I used the names of colors described in the standard color chart (Villalobos system) published in Volume 1 of the "Handbook of North American Birds" (Palmer, 1962). For descriptions of patterns, I used the terminology of Hogan-Warburg (1966). When describing males in the field, I recorded the basic color, secondary color, and pattern of both the neck ruff and head tufts. The basic color is the predominant color of the feathers. The secondary color is the less extensive color, and, when present, creates the pattern. Three primary types of patterns were designated. Combinations of two or more patterns may occur:

(1) *Transverse stripes.*—The secondary color is uniformly distributed as numerous parallel stripes or bars on each feather. The transverse striping may be fine or broad, according to the width of the bars and distance between bars (Figure 1A).

(2) *Spots and blotches.*—Single or multiple secondary colors occur on one feather or a patch of feathers, creating patterns of irregular shapes and sizes. Two size categories are designated. A spot is one centimeter or less in diameter at the widest part (Figure 1B). A blotch is greater than one centimeter in diameter at the widest part (Figure 1C). Spots and blotches usually occur in low numbers and can be counted. Many dense blotches, too numerous to count, are called multiple blotches (Figure 1D).

(3) *Bib.*—The secondary color forms a solid zone on the upper ruff feathers just below the chin, creating a bib of varying length (Figure 1E). When more than one secondary color is present, a layered pattern may be formed. In this case, the bib is the uppermost layer, the basic-colored ruff is the middle layer, and an underneath layer of feathers with another secondary color appears at the bottom of the ruff (Figure 1F).

The nuptial plumages of all resident males and satellite males on SP Lek 1971, SP Lek 1972, and TP Lek 1972 (Tables 2, 3, and 4, respectively) are described according to the standardized method presented above.

Description of Terms

Display territory.—A small area on the lek 20 to 40 centimeters in diameter, the territory is worn or bare ground that is consistently occupied by a resident male. The term "display territory" is equivalent to the term "residence" used by Hogan-Warburg (1966) and van Rhijn (1973). Resident males use the display territories only for courtship display and copulation. Display territories on a lek are separated from one another by a non-defended region (50 to 150 cm wide) called the inter-territorial zone, a term equivalent to "inter-residential" zone of Hogan-Warburg (1966).

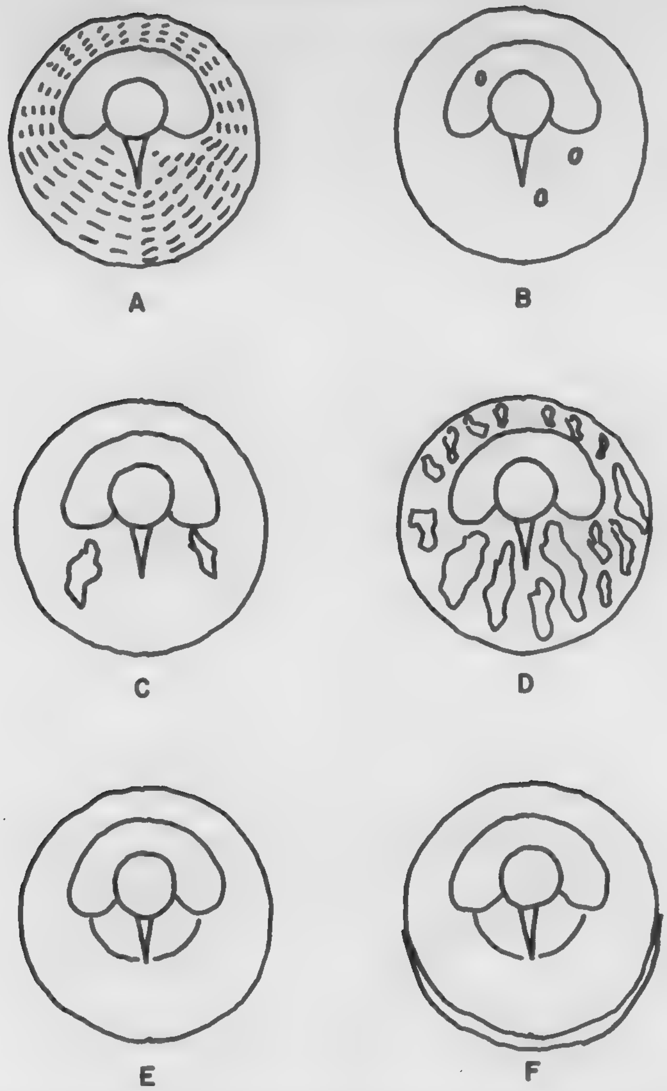

Figure 1. Diagrams showing the types of patterns in the nuptial plumage of male Ruffs. The patterns illustrated are used singly or in combination to describe ruff and head tuft patterns among the polymorphic males. Diagramatically, the large outer circle represents the ruff, the smaller inner circle is the head of the bird with the bill pointing downward, and the semi-circular area above the head indicates the head tufts. A, transverse striping; B, spots; C, blotches; D, multiple blotches; E, bib; F, layers. All patterns except E and F can occur in both ruff and head tufts.

The positions of display territories on a lek were mapped daily. Following the terminology of Hogan-Warburg (1966), I described the positions of display territories by their compass locations and their relationships to one another. A central display territory was surrounded by neighboring territories on all sides. An edge display territory was incompletely surrounded by two or more neighboring territories.

Female visit.—I recorded female behavior and movements on the lek in detail. A female visit is regarded as the presence of a female at a display territory for some period of time. For each female visit to a display territory, data were collected on the location and name of owner of the display territory, the duration of the visit, and the outcome of the visit.

Female preference.—More females visit certain display territories than others on the same lek. I totaled daily the number of female visits to each display territory. Female preference was determined per day by the display territory that received the highest number of female visits on that day.

Satellite male visit.—I defined this visit as the presence of a satellite male on a display territory together with the resident male owner for some period of time. Data were gathered on the location and owner of the display territory visited, the duration of each visit, and the outcome of each visit.

Simultaneous visit by female and satellite male.—A female and a satellite male do not necessarily arrive or depart together, but the overlap in their visits to a display territory results in a simultaneous visit. Thus, I recorded the uninterrupted presence of a female(s) and satellite male(s) on the same display territory at the same time as a simultaneous visit.

TABLE 2
Plumage Descriptions of Males on Lek SP 1971

Male	*Basic and secondary color of head tufts*	*Pattern of head tufts*	*Basic color of ruff*	*Secondary color of ruff*	*Pattern of ruff*	*Wattle color*	*"Dark" or "light"*[1]
Resident males							
WS*[2]	White (Black)	Fine transverse striping	Black	White	Spots (few)	Medium gray	Light
OT*	Orange		Black	Orange	Multiple blotches	Yellow	Light
SB*	Black		Black	Orange-buffy brown	Transverse striping	Yellow	Dark
RM	Black		Scarlet-orange	Black	Transverse striping	Yellow	Dark
GS	Black		Black	White	Transverse striping	Yellow	Dark
CM	White (Black)	Sparse transverse striping	Black	White	Multiple blotches	(not recorded)	Light
OSB	Black		Black	Orange-yellow	Transverse striping	Orange	Dark
BT[3]							
SP	Black		White	Black	Transverse striping	Yellow	Dark
Satellite males							
PS	White (Brownish red)	Two blotches	White			Orange-pink	Light
YG	Brownish red (White)	White tips	White	Brownish red	Layer from underneath	Yellow	Dark
HD	White		White			Yellow	Light
CT	Brownish red (White)	Spots and white tips	White	Brownish red	Blotches	Orange-yellow	Dark

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[1] Classification of male nuptial plumage types follows van Rhijn's (1973:184-185) method. "Dark" males include (1) resident males with "typical independent" plumages with basically black head tufts and ruffs of any color, and (2) satellite males with "untypical" plumages, or those whose colors and patterns do not fall into the category of being either "typical independent" or "typical satellite." "Light" males include (1) resident males with "untypical" plumages, and (2) satellite males with "typical satellite" plumages with plain white ruff and head tufts, or basically white ruff and head tufts with a pattern in either but not both.

[2] Asterisk (*) indicates a successful male (see Table 5).

[3] Undescribed male.

Resident male behavior.—I identified the male courtship behaviors performed in response to females according to the descriptions by Hogan-Warburg (1966). Three behavioral parameters, which I considered to be important for stimulating females due to their consistent performance during female visits, were chosen for quantitative comparison among resident males.

(1) Alternation of static and active behaviors (ALT). Static behavior refers to the Squat. For a detailed description refer to Hogan-Warburg (1966:209-210) and the excellent diagram by van Rhijn (1973, Figure If). The Squat is a horizontal posture in which the legs are folded beneath the body so that the belly and breast of the male lie on the ground. The tip of the bill points vertically downward and may touch the ground, or it is placed on top of the head of a satellite male Squatting with the resident male. The wings are folded over the tail, which may be slightly elevated off the ground. The ruff and head tufts are erected. Active behavior refers to any behavior that results in the male rising from the Squat. Active behaviors interrupt the Squat, and cause an alternation of static and active behaviors. This tendency to alternate behaviors indicates the responsiveness of the resident male to events occurring on the lek. A number of events stimulate a male's active behavior, including female visits to the male's display territory, females elsewhere on the lek, presence of satellite males, activity of other resident males, proximity of marginal males, and arriving conspecifics.

(2) Low Horizontal posture (LH). This behavior is similar to the Squat, except that the body is raised from the ground by a slight stretching of the legs. The tail may be spread and trembled. The wings are folded but may be held out from the tail to expose trembling. The male interrupts the Squat to perform the Low Horizontal posture, which is therefore considered to be an active behavior. Hogan-Warburg (1966:210) described this behavior more fully and van Rhijn (1973, combination of Figures Ie and If) illustrated it. The Low Horizontal was performed only during female visits to

TABLE 3
Plumage Descriptions of Males on Lek SP 1972

Male	*Basic and secondary color of head tufts*	*Pattern of head tufts*	*Basic color of ruff*	*Secondary color of ruff*	*Pattern of ruff*	*Wattle color*	*"Dark" or "light"*[1]
Resident males							
WS*[2]	White (Black)	Fine transverse striping	Black	White	Spots (few)	Medium gray	Light
SB	Black		Black	Scarlet-orange	Transverse striping	Orange-yellow	Dark
WZ	Black		Black	White	Transverse striping and blotches	Yellow	Dark
RM	Black		Brownish red	Black	Transverse striping	Orange-yellow	Dark
OM	Scarlet-orange		Black	Light scarlet-orange	Blotches (oval)	Orange-yellow	Light
Satellite males							
MT[3]	Buffy brown, cream		White			(not recorded)	Light

[1] See Table 2 for explanation of "dark" and "light" categories.

[2] Asterisk (*) indicates successful male (see Table 5).

[3] This satellite male was an extremely infrequent visitor to the lek, and I therefore did not consider it as contributing to the "darkness" or "lightness" of the lek.

territories, when males rose from the Squat and held the Low Horizontal before performing some other behavior. The Low Horizontal, therefore, appears to be the most specific measure of male responsiveness to a female.

(3) Turning Around (TA). The body is turned from side to side or in a circle by trampling movements of the bent legs while the male is in a Low Horizontal posture. During female visits, I recorded Turning Around either when a male turned around or circled a visiting satellite male.

Display rate.—In quantifying displays, I counted the number of times per minute that a resident male performed a behavior pattern during female visits to his display territory. Display rates of all resident males were calculated for each of the three behavior parameters (ALT, LH, and TA). I obtained the mean display rate of a resident male for a specific behavior by dividing the total number of each behavior performed during female visits to the male's display territory throughout the study period by the total minutes of female visits to the male's display territory over the entire study period. The mean display rates of resident males were compared.

Successful male.—The success of a male was determined by the number of females that solicited for copulation, rather than the frequency of the male's copulating attempts. Since a female indicated her choice of a copulation partner by soliciting on a particular display territory, a male had to successfully attract and stimulate a female to solicit before he had an opportunity to copulate.

TABLE 4
Plumage Descriptions of Males on Lek TP 1972

Male	*Basic and secondary color of head tufts*	*Pattern of head tufts*	*Basic color of ruff*	*Secondary color of ruff*	*Pattern of ruff*	*Wattle color*	*"Dark" or "light"*[1]
Resident males							
ST*[2]	Black		Black	White	Transverse striping and bib	Scarlet	Dark
CR*	Chestnut		Black	White	Blotches	Yellow, medium gray	Light
OE*	Scarlet-orange		Black			Orange-yellow	Light
DD	Buffy brown (Brownish red)	Transverse striping	White	Buffy brown	Fine transverse striping	Scarlet	Light
MN	Chestnut		Black			Yellow, medium gray	Light
Satellite males							
CP	White		White			Orange-yellow	Light
GG	Brownish red		White	Brownish red	Layered white ruff with brownish red under-layer	Scarlet red	Dark
MT	Buffy brown, cream		White			(not recorded)	Light

[1] See Table 2 for explanation of "dark" and "light" categories.
[2] Asterisk (*) indicates successful male (see Table 5).

I recorded a female solicitation every time a female crouched at a male's display territory, regardless of whether or not copulation took place, because the act of soliciting indicated female choice. Successful males were those that received the most solicitations from females.

Selection of Display Territories by Females

Females distributed their visits unevenly among the display territories on a lek. The skewed selection of display territories indicated female preference for certain display territories. On any given day during the study period, strikingly more female visits were made to one or two particular display territories than to other display territories on the same lek. The daily total numbers of female visits (V) to each display territory on SP Lek 1971, SP Lek 1972, and TP Lek 1972 are shown in Figures 2, 3, and 4, respectively.

The pattern of territory selection by females varied among the three leks. Female preference shifted from one display territory to another on SP Lek 1971 and TP Lek 1972, while female preference remained stable on SP Lek 1972 (Figures 2, 3, and 4). On SP Lek 1971, females preferred the display territory of Male WS from 2 to 5 May, the territories of Males WS and OT on 6 and 7 May, Male OT's during 8 and 9 May, Male SB's on 10 and 11 May, both Male SB's and Male WS's on 12 May, both Male SB's and Male OT's on 13 May, and Male SB's display territory on 14 and 15 May. On TP Lek 1972, females preferred the display territories of the following males: Male ST, 6 May; Males OE and CR, 7 and 8 May; Male CR, 9 May; Male OE, 10 May; Male DD, 13 May; Male ST, 14 May; Males ST, DD, and MN, 15 May; Male ST, 16 May. On SP Lek 1972, females preferred the same display territory throughout the study period, although a change in resident male ownership occurred. From 2 through 9 May, Male WS owned the preferred display territory. Then Male WS was displaced by Male OM, who held the display territory from 11 through 13 May. Females still preferred this territory during its occupation by Male OM.

Resident Male Success

The success of resident males was measured by the number of females stimulated to solicit for copulation at males' display territories. A female that solicited at a display territory afforded the resident male, or resident male and visiting satellite male(s), the opportunity to copulate. Whether a male succeeded in copulating depended on the appropriate response by the male to the female, and on other variable factors subsequent to the female's solicitation behavior.

Success was unevenly distributed among the resident males on a lek. The numbers of female solicitations differed markedly at different display territories (Table 5). The same resident males whose display territories were preferred for female visits (Figures 2, 3, and 4) also received the highest percentages of female solicitations.

Location of Display Territories

The relationship between the position of the display territory on the lek and the success of the resident male owner in attracting and stimulating females to solicit varied among the three leks studied. I found no consistent association between the location of a certain display territory and resident male success. Rather, a different situation existed on each lek. On SP Lek 1971 (Figure 2), the central display territories were most successful from 2 to 7 May (Male WS, then

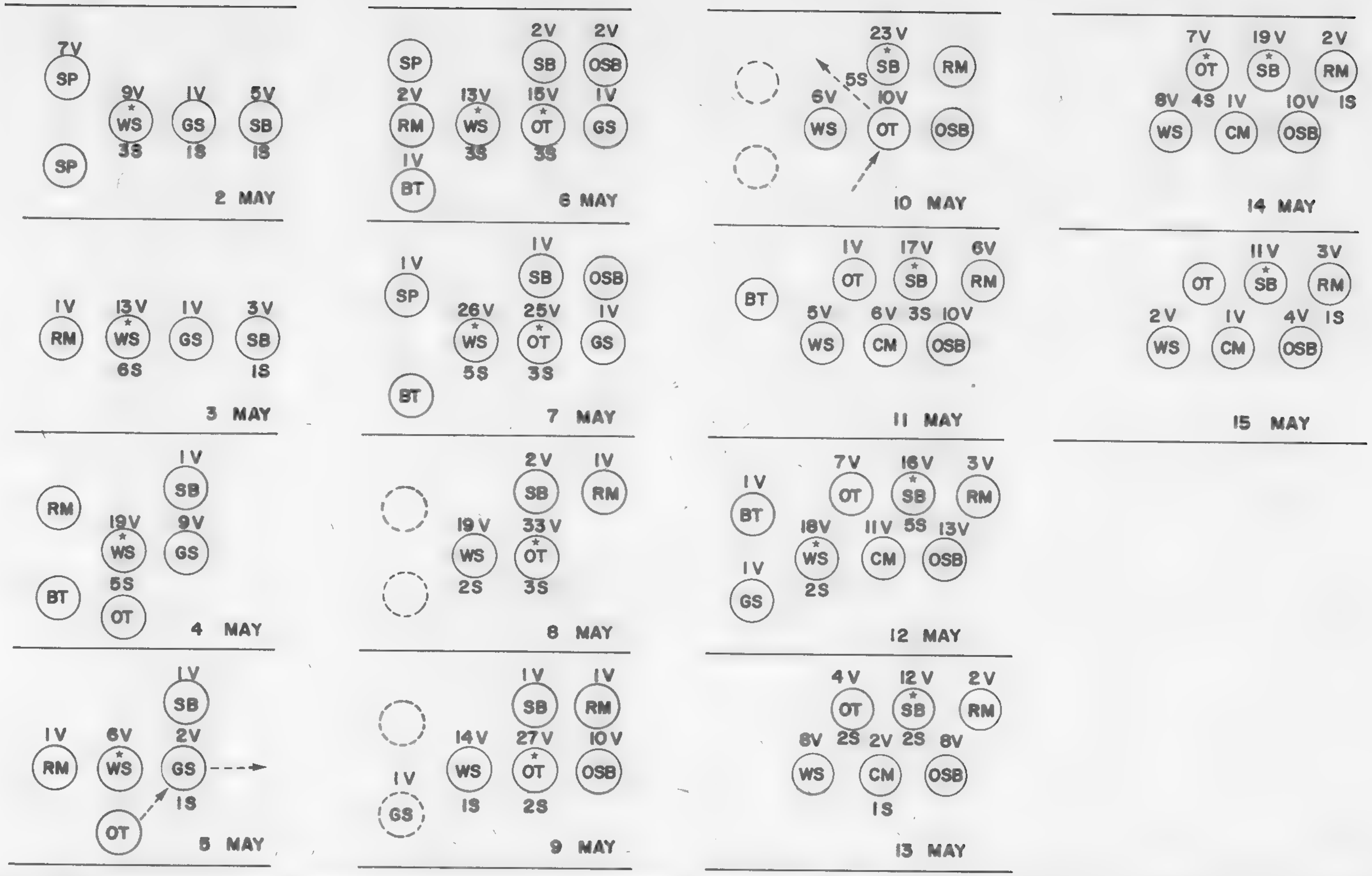


Figure 2. Lek SP 1971. Daily maps of lek configuration showing the changes in location and ownership of display territories by resident males during the course of the season. Solid-line circles represent established, occupied display territories. Dotted-line circles are previously or infrequently occupied display territories. Capital letters within the circles designate the resident male owners. Dotted-line arrows show the direction of change of display territory location or ownership. Female preference is indicated by the number of visits and solicitations at each display territory. The total daily number of female visits to a display territory is the value of "V" directly above the territory. The total daily number of female solicitations for copulation at a display territory is the value "S" directly beneath the territory. The most successful males are indicated by asterisks (*). The sequence of maps shows the shift of female choice during the course of the season (follow the asterisk). The figure is not drawn to scale. Display territory size averages 20 to 40 cm in diameter. Average distance between display territories is 50 to 150 cm.

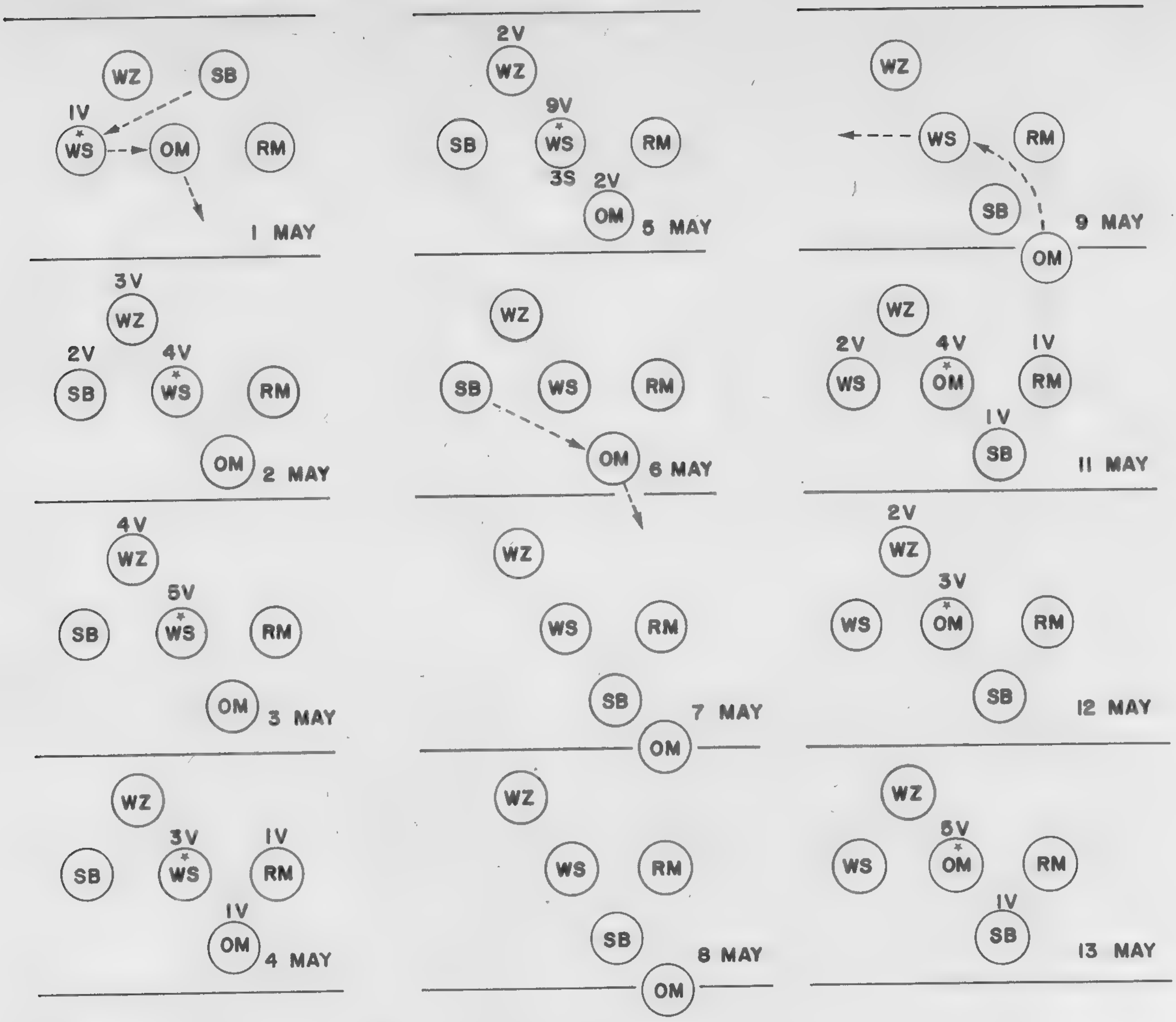


Figure 3. Lek SP 1972. Daily maps of lek configuration showing the changes in location and ownership of display territories by resident males during the course of the season. Solid-line circles represent established, occupied display territories. Capital letters within the circles designate the resident male owners. Dotted-line arrows show the direction of change of display territory location or ownership. Female preference is indicated by the number of visits and solicitations at each display territory. The total daily number of female visits to a display territory is the value of "V" directly above the territory. The total daily number of female solicitations for copulation at a display territory is the value of "S" directly beneath the territory. The most successful males are indicated by asterisks (*). The sequence of maps shows the consistent preference of females for the central display territory (follow the asterisk). The figure is not drawn to scale. Display territory size averages 20 to 40 cm in diameter. Average distance between display territories is 50 to 150 cm.

Males WS and OT), after which edge display territories became most successful (8 to 15 May: Male OT, then Male SB). On SP Lek 1972 (Figure 3), the central display territory was most successful throughout the entire study period (Male WS, then Male OM). On TP Lek 1972 (Figure 4), a succession of different edge display territories was most successful.

Behavior of Resident Males

Males on each lek showed differences in the display rates of certain behaviors: Low Horizontal, Turning Around, and the alternation of static and active behaviors. Figures 5, 6, and 7 show the mean display rates of these behaviors for all resident males, plotted as a function of success in stimulating female solicitation.

The relationship between resident male success in stimulating females to solicit and resident male display rates was similar on all three leks. Successful resident males typically showed intermediate and high display rates (Figures 5, 6, and 7). Looking at display rates from the three leks combined, the overall range of display rates for Low Horizontal was as follows: rate of display, 0.00 to 0.92 per minute; range of success, 0.17 to 0.82 displays per minute. The overall range for Turning Around: rate of display, 0.00 to 1.33 per minute; range of success, 0.19 to 0.90 displays per minute. The overall range of alternating static and active behaviors: rate of Alternation, 0.00 to 2.11 per minute; range of success, 0.58 to 2.11 alternations per minute. Males with low rates of display were unsuccessful in all cases.

On all three leks, display rates for Turning Around and Low Horizontal of all successful males fell within the intermediate to high value range (Figures 5 and 6). On two of three leks, display rates for alternating static and active behaviors of all successful males fell within the intermediate to high value range (Figure 7). An exceptional male was Male WS on SP Lek 1972. This male exhibited the highest display rate observed (Figure 7), and was the only successful male on SP Lek 1972. Five resident males with intermediate to high display rates were unsuccessful, possibly due to other factors. Male CM appeared on the lek late in the season; male MN also appeared on the lek late in the season and received only one female visit; Males DD and OM were very inactive during the first half of the study period before their activity increased; and Male SB 72, although showing relatively high display rates for Turning Around and alternation of static and active behaviors in general, performed low rates of Low Horizontal, possibly indicating a poor response to females specifically.

Satellite Male Visits

The numbers of satellite male visits were unevenly distributed among the territories on a lek. Satellite males, like females, exhibited preferences for certain display territories (Table 6). Those resident males that were most successful in stimulating females to solicit also had either medium or high percentages of satellite male visits, indicating some degree of overlap between the preferences of females and satellite males for the display territories of resident males.

Simultaneous Visits by Females and Satellite Males

On each lek, females and satellite males showed an uneven distribution of simultaneous visits to display territories. Certain territories attracted females and satellite males simultaneously more frequently than others (Table 7).

The relationship between the success of resident males in stimulating females to solicit and the frequency of simultaneous female and satellite male visits to display territories differed among the three leks (Tables 5 and 7). On SP Lek 1971, a positive correlation existed between resident male success and the frequency of simultaneous visits by females and satellite males. The three most successful resident males (SB, WS, and OT) had the highest percentages of simultaneous visits by females and satellite males to their display territories. Females solicited most frequently at display territories jointly occupied by resident male and satellite male(s). On SP Lek 1972, I found no correlation between resident male success and frequency of simultaneous visits by females and satellite males. At this lek, I did not see females soliciting at any display territories during the brief period (11 to 13 May) when satellite

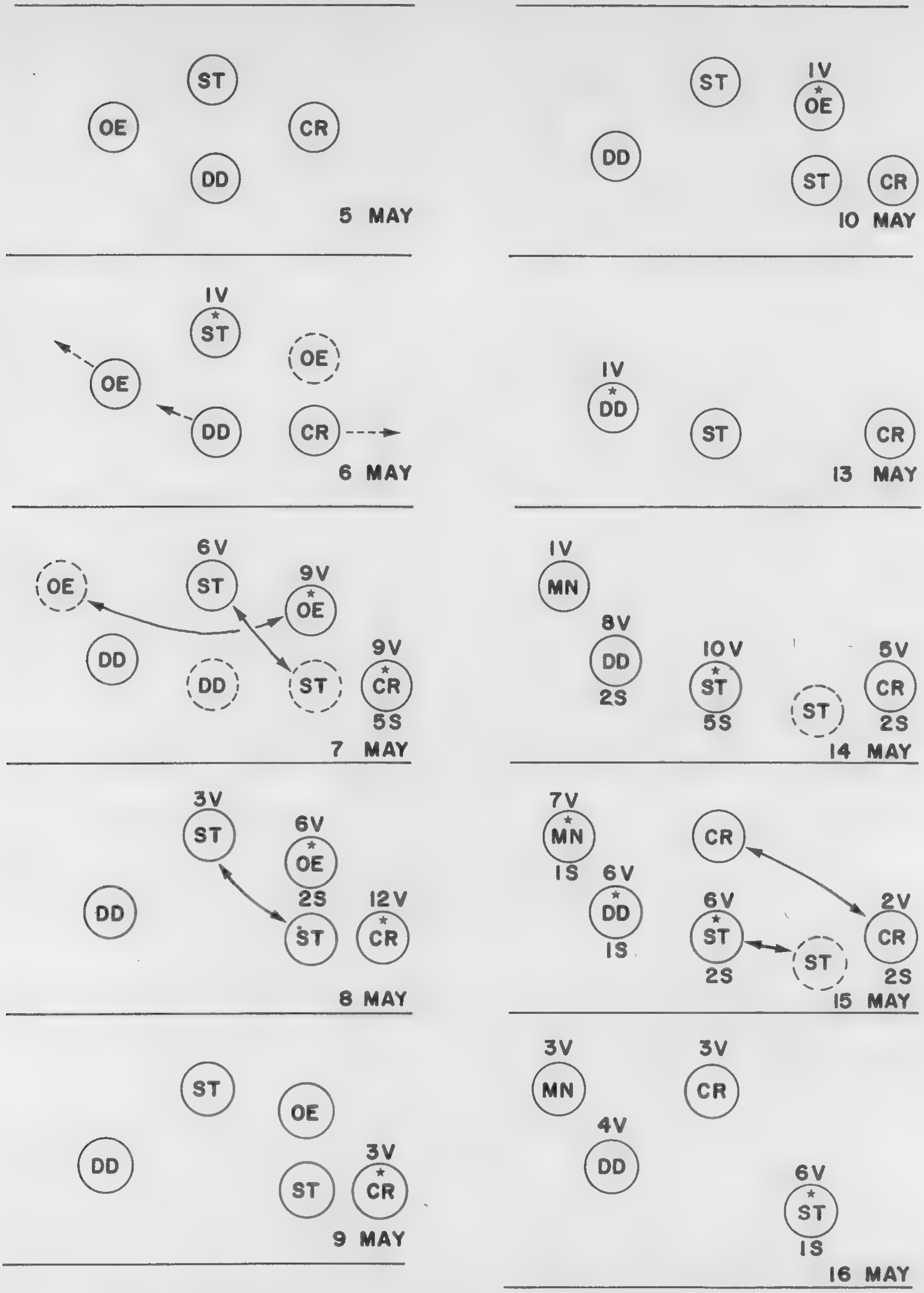


Figure 4. Lek TP 1972. Daily maps of lek configuration showing the changes in location and ownership of display territories by resident males during the course of the season. Solid-line circles represent established, occupied display territories. Dotted-line circles are infrequently occupied display territories. Capital letters within the circles designate the resident male owners. Dotted-line arrows show the direction of change of display territory location. Solid-line arrows indicate that a resident male owns two display territories. Female preference is determined by the number of visits and solicitations at each display territory. The total number of female visits to a display territory is the value of "V" directly above the territory. The total daily number of female solicitations for copulation at a display territory is the value of "S" directly beneath the territory. The most successful males are indicated by asterisks (*). The sequence of maps shows the shift of female choice during the course of the season (follow the asterisk). The figure is not drawn to scale. Display territory size averages 20 to 40 cm in diameter. Average distance between display territories is 50 to 150 cm.

males visited the lek. On TP Lek 1972, my data show no conclusive relationship between resident male success and the frequency of simultaneous visits by females and satellite males. I found that successful males had both high (45.0 percent, Male CR) and low (9.1 percent, Male OE) percentages of simultaneous visitations. Thus, on some display territories, female solicitation occurred only in the presence of a satellite male with the resident male, while at others it did not. Furthermore, females did not solicit on some territories with, or without, satellite males.

Discussion

The methods by which females choose partners for copulation are determined by the nature of the mating system. In the lek mating system of the Ruff, no pair-bond is established between male and female, and the sexes have very little contact except when females visit a lek. Consequently, I suggest females probably require a high degree of male stimulation for rapid development of reproductive physiology and behavior. The elaborate nuptial plumage and display behavior of the males on the lek provide this stimulation. A female visiting the lek for the first time walks around probably "testing" the different stimulus situations created by males on the display territories. After a variable number of visits to the lek, a female finds a situation that successfully stimulates her to solicit for copulation.

Some resident males were more successful than others in attracting females and in stimulating them to solicit for copulation (Figures 3, 4, and 5; Table 5). In other words, certain stimulus situations elicited greater responses from females than others. In addition, I observed a turnover of successful males during the course of the display season (Figures 3, 4, and 5). I suggest that female preference for males shifted to parallel the changing location of the successful stimuli during the season.

Optimal Stimulation

My results presented several potential sources of stimulation for females in relation to resident male success. The variability in the results from lek to lek was striking. All the factors investigated as potential stimuli for females correlated to some degree with resident male success. However, the specific factors for male success varied among the three leks. This finding leads me to hypothesize that females choose partners for copulation on the basis of an optimal stimulus situation. One expects a female to solicit for copulation at the display territory that most optimally stimulates her. The specific factors composing the stimulus situation and the absolute level of its intensity should not be important to the female. Rather, she probably compares the relative stimulus intensities emanating from each of the display territories on a given lek, and chooses the territory that provides the optimal stimulation. A male should thus be able to stimulate successfully female solicitation through any combination of stimulus factors, as long as the relative intensity of stimulation is optimally high. This hypothesis could explain the observed variation in the factors characterizing successful males on Ruff leks. If the female simply responds to an optimal stimulus situation, the component factors producing the necessary stimulation could vary from lek to lek, as well as through time on the same lek.

An optimal stimulus situation is superior to a maximal one, since the latter actually may have a negative effect on females' solicitation. Hogan-

Warburg (1966) described the fear reaction of females when resident males engage in heavy fighting. Van Rhijn (1973) showed that too much activity can inhibit solicitations by females. This suggests that a very high level of stimulation may actually induce fear in females. Optimal stimulation must be high enough to attract and stimulate a female but not so high that she is frightened away. It seems reasonable to assume that the stimulation level optimal for a female varies among individual females according to age, experience, and stage of reproductive development. Possibly successful males are better able than unsuccessful males to judge the amount of stimulation a female requires to solicit without becoming frightened. Kruijt *et al.* (1972) observed that a successful male Black Grouse *(Lyrurus tetrix)* approached a female entering his territory, but withdrew when the female began to leave the territory. Withdrawal possibly reduced the fear of the female and allowed her to return to the male.

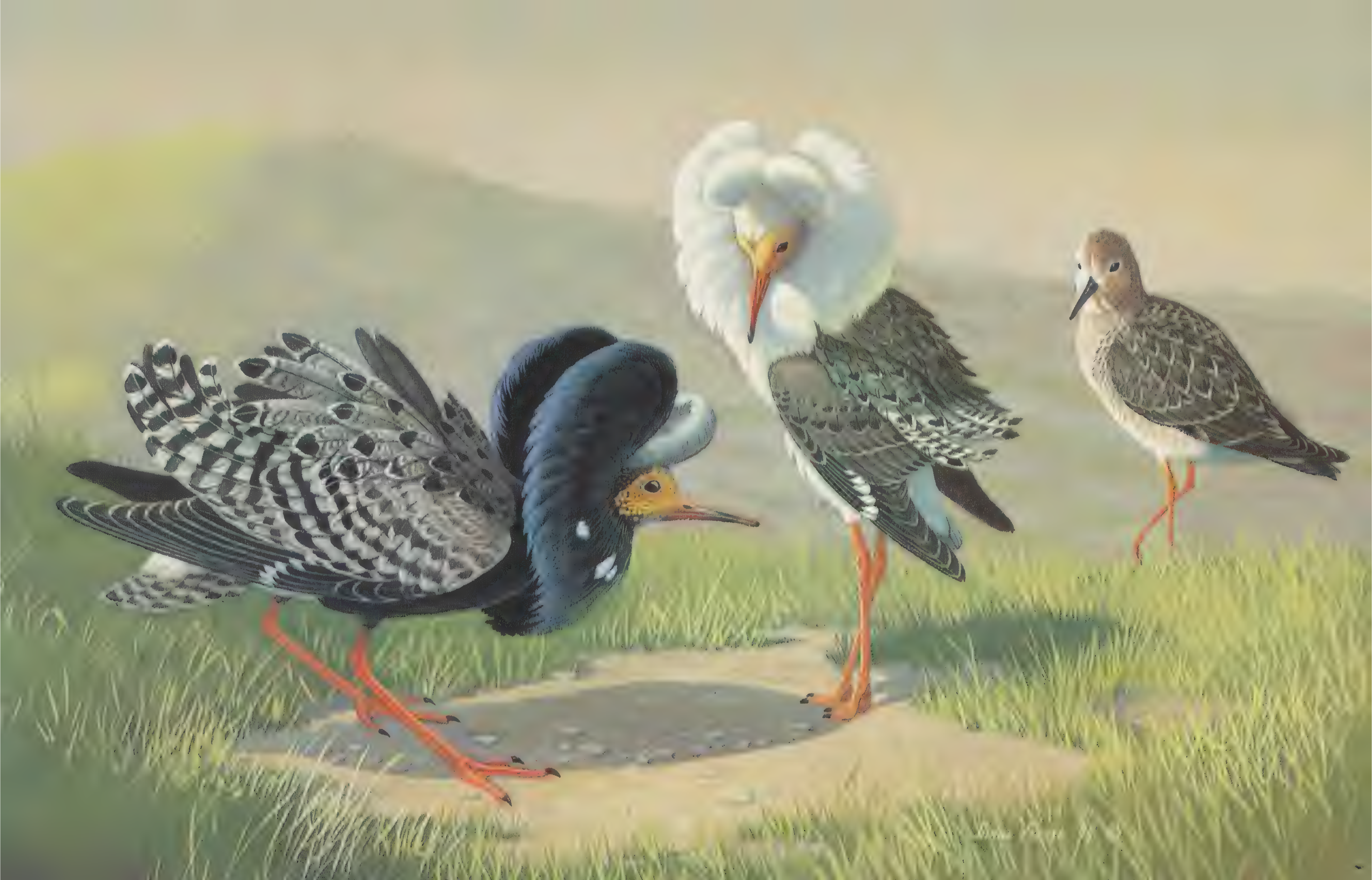
Location of the Display Territory

The central location of a display territory may be a factor in stimulating females according to a density gradient. Male density increases from the edge to the center of the lek. Stimulus intensity also should increase toward the center of the lek. At the central display territory a female receives stimulation from the central resident male plus all the surrounding males. Thus females may be optimally stimulated to solicit at the central display territory if other stimuli emanating from other display territories are equal.

My data showed that the central territory position sometimes correlated with male success in stimulating female solicitation. On Lek SP 1971, the male holding the central territory was most successful for eight consecutive days. And females continued to prefer the central territory even when the geometrical center of the lek shifted. Due to the temporary absence of edge resident males (Figure 3: 8 and 9 May), the original central display territory became an edge territory; the female preference simultaneously shifted to the new central territory. Later in the study period, edge display territories became most successful, indicating that factors other than central location of the territory may have become more effective in stimulating females. On SP Lek 1972, females consistently preferred the central display territory, and males "coveted" the central location. Male OM only became successful in attracting females after he had displaced Male WS from the central display territory (Figure 4). On TP Lek 1972, the geometrical arrangement of the display territories did not create a central territory, so that females probably responded to other sources of stimulation for solicitation.

Hogan-Warburg (1966) also reported different relationships between display territory locations and the frequency of female solicitations and copulations. On one of her large leks, the most preferred territory had a central position; on another large lek, the two most preferred territories had edge positions. Bancke and Meesenburg (1958) mapped territory positions weekly and recorded copulation success of resident males on Ruff leks in Denmark. Their data did not indicate a close relationship between display territory location and male success, the central display territory being most successful in only two out of ten samples. Kruijt *et al.* (1972), on the other hand, found a strong preference by females for central males on Black Grouse leks. Wiley (1973) reported a consistent correlation in Sage Grouse *(Centrocercus urophasianus)* between the central territory and copulation success of males.

Ruff, *Philomachus pugnax.* Painting by Diane Pierce.



In contrast, Hartzler (1972) studied the same Sage Grouse leks and found that copulation success of males shifted from one cock to another and did not correlate with geographic location on the lek. Thus it appears that on some leks the centrally located territory is a major factor in stimulating female solicitation, while on other leks different factors must be influencing females.

Resident Male Behavior and Female Stimulation

Behavioral characteristics of resident males are a potential source of stimulation for females. On leks where quantitative behavioral differences exist among the males, some resident Ruffs possibly stimulate females more effectively than other males. Females could use a behavior or activity gradient to direct them to the territory that most optimally stimulates them to solicit for copulation.

Hogan-Warburg (1966) made the qualitative observation that on both large and small Ruff leks, females copulated with "risers" rather than with "squatters." Males that interrupted the Squat more readily to perform active behaviors were more successful in stimulating females to solicit than others that remained in a Squat during female visits to their display territories. Hartzler (1972) reported that high strutting rates of Sage Grouse cocks correlated with

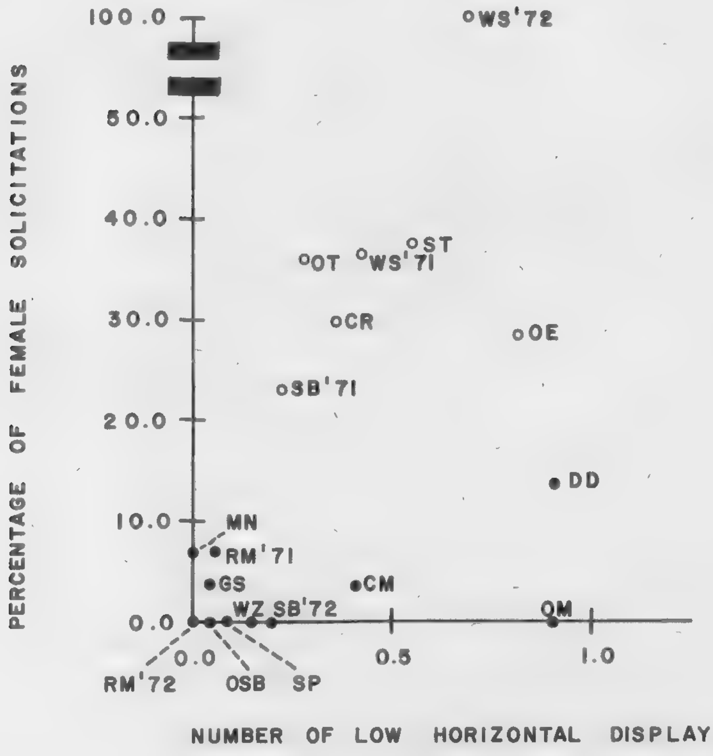
TABLE 5
Female Solicitations
at Each Resident Male's Display Territory

Male	*Percentage of female solicitations*	*Number of female solicitations*	
		On display territory	*On lek*
	SP Lek 1971		
WS	37.0	27[1]	73[2]
OT	36.4	20	55
SB	23.3	17	73
RM	6.8	5	73
GS	4.1	3	73
CM	4.0	1	25
OSB	0.0		
BT	0.0		
SP	0.0		
	SP Lek 1972		
WS	100	3	3
SB	0		
WZ	0		
RM	0		
OM	0		
	TP Lek 1972		
ST	38.1	8	21
CR	33.3	7	21
OE	28.6	2	7
DD	14.3	3	21
MN	7.1	1	21

[1] The total number of female solicitations at the display territory of resident male.

[2] The total number of female solicitations on the lek during the resident male's tenure on the lek.

male copulation success, while unsuccessful cocks typically performed lower strutting rates. My data supported the results of Hogan-Warburg (1966) and Hartzler (1972). I found (Figures 5, 6, and 7) that high display rates, or frequent interruption of the Squat, correlated positively with resident male success in stimulating females to solicit. Males with low display rates, i.e., those that rarely interrupted the Squat, were unsuccessful in stimulating female solicitation. Low Horizontal display rates were the most specific measure of the tendency of resident males to rise from the Squat and perform active behavior toward a visiting female. This indicated the male's responsiveness to the female. Turning Around display rates included the response of the resident male to the presence of satellite males simultaneously with females on the display territory. Therefore, this measured the readiness of the resident male to perform active behavior directed to either the female or satellite male. Rates of alternation of static and active behavior were the most general measures of activity for resident males since they included responses to anything on or off the lek that caused males to interrupt the Squat. However, all three measures (Low Horizontal, Turning Around, and alternation of static and active behaviors) showed a similar correlation between high display rates and male success in stimulating female solicitation. The consistently positive relationship on all



LEK SP'71

A	B	C D
CM	0.42	(18/43)
* WS	0.41	(175/428)
* OT	0.25	(90/364.5)
* SB	0.17	(49/280.75)
SP	0.06	(1/15.5)
OSB	0.05	(8/164.5)
RM	0.04	(3/75.75)
GS	0.04	(2/51)

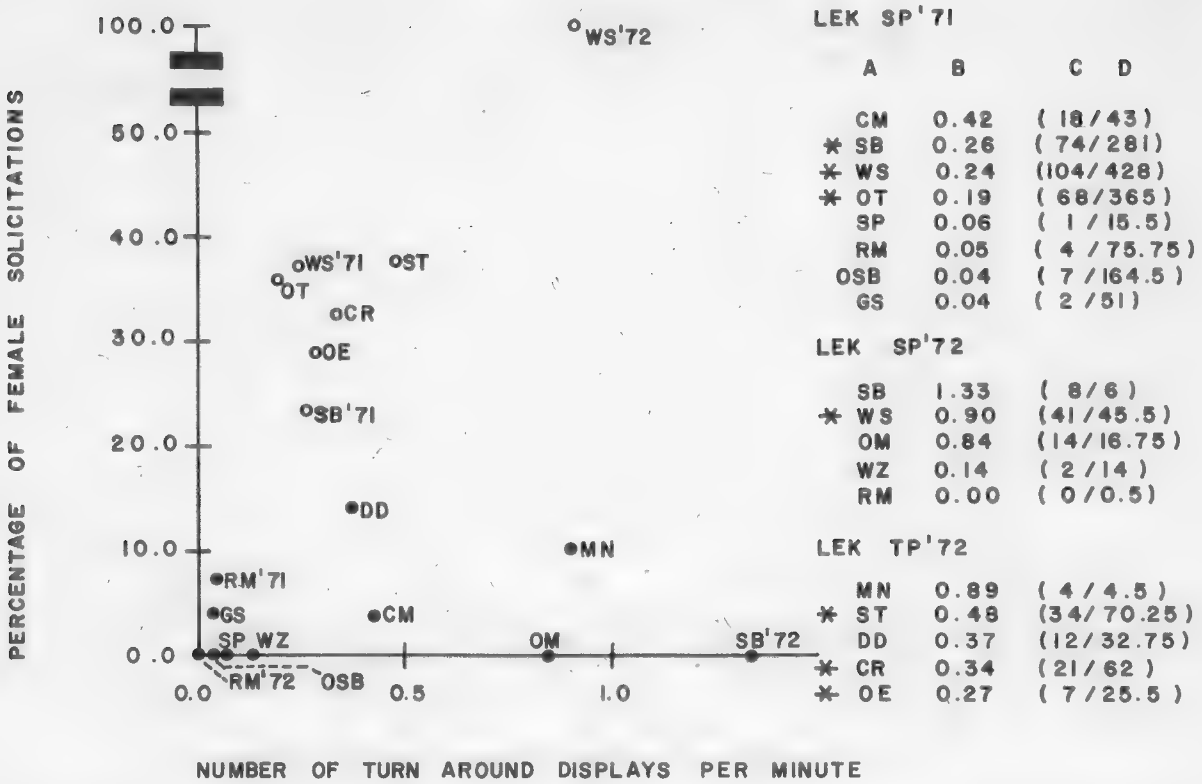
LEK SP'72

A	B	C D
OM	0.90	(15/16.75)
* WS	0.66	(30/45.5)
SB	0.17	(1/6)
WZ	0.14	(2/14)
RM	0.00	(0/1.5)

LEK TP'72

A	B	C D
DD	0.92	(30/32.75)
* OE	0.82	(21/25.5)
* ST	0.54	(38/70.25)
* CR	0.34	(21/62)
MN	0.00	(0/4.5)

Figure 5. Relationship between Low Horizontal display rates of resident males and resident male success in stimulating females to solicit for copulation. Open circles are successful resident males. Closed circles are unsuccessful resident males. Capital letters identify the individual resident males. Males present on a lek more than one year are differentiated by the suffix '71 or '72. The same data presented in the graph are listed on the right according to lek, and the successful males are indicated by asterisks (*). Column A, resident male; column B, mean number of Low Horizontal displays performed per minute by a resident male during female visits to his display territory; column C, total number of Low Horizontal displays performed by a resident male during all female visits to his display territory throughout the study period; column D, total number of minutes of female visits to a resident male's display territory throughout the study period. The Low Horizontal display rate is the most specific measure of male responsiveness to a female visiting the display territory. The graphed data show that successful resident males exhibit intermediate to high display rates, while unsuccessful males have predominantly low display rates. Three males were exceptions. Male CM did not join the lek until late in the season, and both Male OM and Male DD did not become active until late in the season.



LEK SP'71

	A	B	C D
	CM	0.42	(18/43)
*	SB	0.26	(74/281)
*	WS	0.24	(104/428)
*	OT	0.19	(68/365)
	SP	0.06	(1 / 15.5)
	RM	0.05	(4 / 75.75)
	OSB	0.04	(7 / 164.5)
	GS	0.04	(2 / 51)

LEK SP'72

	A	B	C D
	SB	1.33	(8/6)
*	WS	0.90	(41 / 45.5)
	OM	0.84	(14/16.75)
	WZ	0.14	(2 / 14)
	RM	0.00	(0/0.5)

LEK TP'72

	A	B	C D
	MN	0.89	(4 / 4.5)
*	ST	0.48	(34/ 70.25)
	DD	0.37	(12/ 32.75)
*	CR	0.34	(21/ 62)
*	OE	0.27	(7 / 25.5)

Figure 6. Relationship between Turn Around display rates of resident males and resident male success in stimulating females to solicit for copulation. Open circles are successful resident males. Closed circles are unsuccessful males. Capital letters identify the individual resident males. Males present on a lek more than one year are differentiated by the suffix '71 or '72. The same data presented in the graph are listed according to lek, and the successful males are indicated by asterisks (*). Column A, resident males; column B, mean number of Turn Around displays performed per minute by a resident male during female visits to his display territory; column C, total number of Turn Around displays performed by a resident male during all female visits to his display territory throughout the study period; column D, total number of minutes of female visits to a resident male's display territory throughout the study period. The Turn Around display rate measures responsiveness to visiting females as well as satellite males, and it is less specific than the Low Horizontal response. The graphed data show that successful resident males exhibit intermediate to high Turn Around display rates, while unsuccessful males have predominantly low display rates. Five males were exceptions. Male CM and Male MN joined the lek late in the season. Male DD and Male OM were very inactive until late in the season. Male SB '72 may have Turned Around too much, using poor courtship tactics.

leks in my study area between high display rates and male success suggests that active behavior of resident males is possibly the most important factor for stimulating females to solicit, regardless of other sources of stimulation.

Van Rhijn (1973, Table 40) showed that resident males can attract more female visits to their territories by performing high rates of "turning" displays and ". . . starting off with 'sequences' of movements (after periods of immobility) . . ." (page 207). However, he also presented data (Table 36) to demonstrate that ". . . high activity level is negatively correlated with crouching of females . . ." (page 202). My data supported the first conclusion of van Rhijn, that high display rates attract more female visits (compare my Figures 2, 3, and 4 with 5, 6, and 7). Females are presumably first attracted by the males' activity before they are stimulated to solicit.

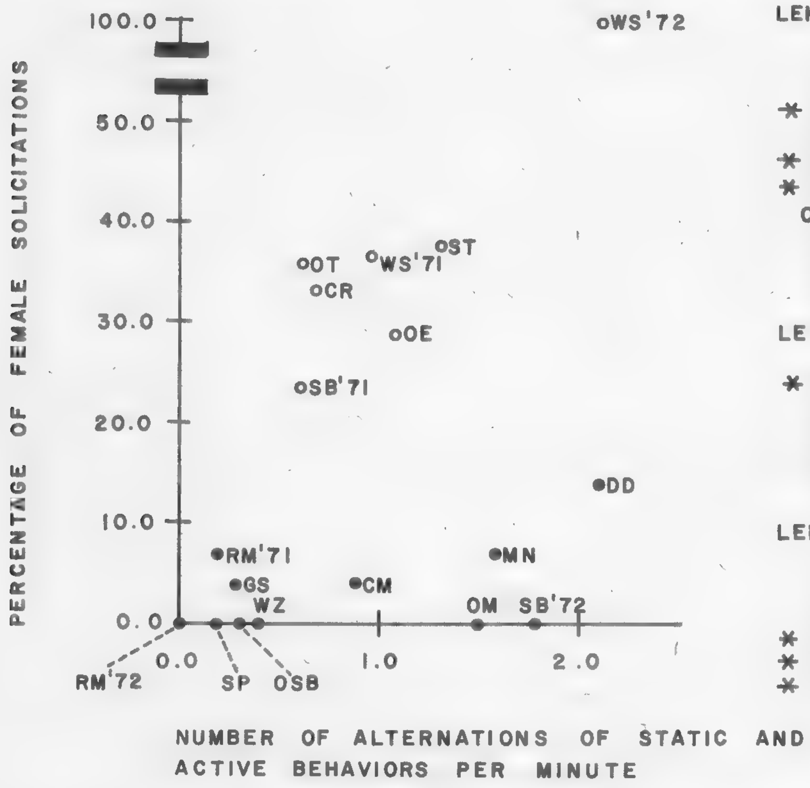
My data did not agree with the second conclusion of van Rhijn (1973) that high male activity is negatively correlated with female solicitation. This may be true at extreme levels of activity, but van Rhijn did not clearly specify the conditions of his statement. Thus, our different results could be due to the interpretation of male activity levels as they are experienced by females. Van Rhijn (1973) compared males in relation to an arbitrarily chosen, absolute cut-off value: males that perform fewer than one activity per minute compared to males that perform one, or more than one, activity per minute. In respect to this fixed cut-off point, van Rhijn's results from several different leks showed a negative correlation between male activity level and female tendency to solicit. This finding is the reverse of what I would expect on the basis of his data, which show that high activity levels of resident males attract more female visits than low activity levels. I also based my measure of display rate on the number of times a behavior was performed per minute during a female visit, but I did not specify an absolute value for display rates against which to judge male success. It seems that females compare relative display rates of all the resident males on a particular lek by experiencing the relative stimulation emanating from each display territory. Females then respond to a male whose display rate is high enough to stimulate solicitation without inducing fear. It is also conceivable that the rates of display among males vary from lek to lek, so that females could not feasibly search for an absolute value of stimulation but must seek out the most optimal situation available on each lek. This requires female response to relative, rather than absolute, values for display rates. My data (Figures 5, 6, and 7) showed that on each lek, a high display rate correlated with male success in stimulating female solicitation, but the range of successful display rates varied from lek to lek.

Wiley (1973) found no quantitative or qualitative differences in strutting rates among lekking Sage Grouse males. Theoretically, it is possible for all males on a lek to be equal behaviorally, so that females would respond to unequal stimulus intensities from other sources, such as a centrally located territory, to discriminate among the males on a lek. The fact that Wiley (1973) found no behavioral differences among males, but that Hartzler (1972) found quantifiable rate differences among strutting males, suggests that the factors stimulating female choice of partners for copulation vary on different leks in Sage Grouse as well as in Ruffs.

Satellite Males and Female Stimulation

The presence of satellite males on resident male territories may increase the intensity of stimuli emanating from these territories. The sum of the stimulation provided by both the resident and satellite males might create a more optimal stimulus for females than that provided by the resident male alone. Hogan-Warburg (1966) observed that, on small leks in particular, females were more attracted to territories having multiple occupancy than those with a resident male alone. Van Rhijn (1973, Table 29) showed that females preferred to visit territories with satellite males on them. My data indicated a high correlation of preference for the same display territories by females and satellite males (Table 6). In terms of stimulating the female to solicit, Hogan-Warburg (1966) found that females on small leks most frequently crouch for, and copulate with, a male on a territory with a resident and at least one satellite male. She also reported that resident males visited by satellite males interrupted the Squat to perform behavior toward the female, satellite male, or other resident males more often that did resident males without satellite males on their territories. Thus females may be more highly stimulated to solicit at a display territory with both resident and satellite males present due to the higher activity level found on that territory.

In contrast, Hogan-Warburg (1966) found that on large leks resident males rarely tolerated satellite males, and that females solicited and copulated most frequently at territories occupied only by resident males. She observed that the most successful resident males on large leks typically interrupted the Squat and performed active behavior directed toward the female more frequently than successful males on small leks. My interpretation would be that these successful males on large leks had intrinsically high display rates capable of stimulating females to solicit without requiring satellite males for additional stimulation. My data (Table 7) from small leks showed that the presence of satellite males may or may not be correlated with success in stimulating females to solicit, depending upon the situation. This suggests that some resident males benefit from having satellite males on their territories, while other resident males can be successful without satellite males. On SP Lek 1971, the simultaneous presence of satellite males and females on a territory correlated positively with male success in stimulating female solicitation. The characteristics of the resident males alone were apparently



LEK SP'71

A	B	C D
* WS	0.95	(405 / 428)
CM	0.88	(38 / 43)
* SB	0.61	(171 / 280.75)
* OT	0.58	(212 / 364.5)
OSB	0.29	(48/ 164.5)
GS	0.29	(15 / 51)
SP	0.19	(3 / 15)
RM	0.17	(13 / 75.75)

LEK SP'72

A	B	C D
* WS	2.11	(96 / 45.5)
SB	1.83	(11 / 6)
OM	1.49	(25 / 16.75)
WZ	0.36	(5 / 14)
RM	0.00	(0 / 1.5)

LEK TP'72

A	B	C D
DD	2.11	(69 / 32.75)
MN	1.56	(7 / 4.5)
* ST	1.34	(94 / 70.25)
* OE	1.06	(27 / 25.5)
* CR	0.73	(45 / 62)

Figure 7. Relationship between resident males' rates of alternation of static and active behavior, and resident male success in stimulating females to solicit for copulation. Open circles are successful resident males. Closed circles are unsuccessful males. Capital letters identify the individual resident males. Males present on a lek more than one year are differentiated by the suffix '71 or '72. The same data presented in the graph are listed according to lek, and the successful males are indicated by asterisks (*). Column A, resident males; column B, mean numbers of alternations of static and active behaviors per minute by a resident male during female visits to his display territory; column C, total number of alternations of static and active behavior by a resident male during all female visits to his display territory throughout the study period; column D, total number of minutes of female visits to a resident male's display territory throughout the study period. The rate of alternation of static and active behavior is the most generalized measure of male responsiveness to all stimuli on the lek. The graphed data show that successful resident males exhibit intermediate to high rates of alternation of static and active behavior, while unsuccessful resident males have predominantly low rates of alternation of static and active behavior. Five males were exceptions. Male CM and Male MN joined the lek late in the season. Male DD and Male OM were very inactive until late in the season. Male SB '72 apparently responded more to stimuli elsewhere on the lek than to the visiting female (compare with the low display rate of this male for Low Horizontal).

TABLE 6
Satellite Male Visits
to Each Resident Male's Display Territory

Male	*Percentage of satellite male visits*	*Number of visits by satellite males*	
		To display territory	*To lek*
	SP Lek 1971		
SB*[1]	29.7	68[2]	229[3]
OSB	19.2	44	229
OT*	17.0	39	229
WS*	11.8	27	229
RM	10.9	25	229
CM	5.2	12	229
GS	3.5	8	229
SP	1.3	3	229
	SP Lek 1972		
RM	50.0	4	8
OM	37.5	3	8
WS*	12.5	1	8
SB	0.0		
WZ	0.0		
	TP Lek 1972		
MN	43.3	20	46
CR*	31.4	21	67
ST*	25.4	17	67
OE*	14.3	3	21
DD	9.0	6	67

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[1] Asterisks (*) indicate successful resident males with the highest percentages of female solicitations.
[2] The total number of visits by satellite males to the display territory of the resident male.
[3] The total number of visits by satellite males to all display territories on the lek during the resident male's tenure on the lek.

not as stimulating for females as when satellite males were also present on display territories. On TP Lek 1972, some resident males benefited from having satellite males (Male CR and Male ST), while one resident male was successful in stimulating female solicitation without the presence of satellite males (Male OE).

Van Rhijn (1973) proposed that cooperation with satellite males would be adaptive for most resident males if they regularly alternated tolerant and intolerant behavior. He presented evidence that resident males become intolerant of satellite males when the frequency of female visits and/or copulations becomes high, and that resident males resume tolerant behavior when female visits and the frequency of copulation decline. He added that "exceptional" resident males, which could successfully attract female visits without the presence of satellite males on their territories, would not benefit from admitting satellites. This hypothesis suggests that resident males of "intermediate" activity levels can increase the stimulus intensity of their display territories by tolerating satellite males, and thereby increase the probability of success in stimulating females to solicit. However, resident males with high activity levels may be able to stimulate females to solicit on their own, so that it would not be to their advantage to tolerate satellite males and compete with them for copulation.

One consequence of the intolerance of successful resident males for satellite males may be that the unsuccessful resident males on adjacent territories may receive more visits from satellite males than would be expected on the basis of female and satellite male preferences. This might explain the high numbers of satellite visits to Male OSB on SP Lek 1971, and Male MN on TP Lek 1972, (Table 6). These unsuccessful males maintained territories close to those of successful males. When the latter became intolerant toward satellite males, the satellites entered the neighboring territories of unsuccessful and tolerant males. Nonetheless, Males OSB and MN did not succeed in stimulating females to solicit at their territories, probably because they had low activity levels. Even the presence of satellite males could not create enough stimulation to attract females away from their more active neighbors.

In contrast to my results and those of Hogan-Warburg (1966), van Rhijn (1973, Table 35) did not find that satellite males had a positive influence on the copulation frequency of resident males. He presented data to show that successful residents had females and satellites simultaneously on their display territories less frequently than did unsuccessful resident males. He concluded that when females are on a display territory the resident male no longer benefits from the presence of a satellite male. My own data (Table 7) gave the opposite results, i.e., that females and satellites simultaneously visited the territories of successful males more frequently than those of unsuccessful males. Thus I concluded that resident males can benefit from the presence of satellite males and females simultaneously on their territories.

The cause of our reversed conclusions may come from our measures of male success. Van Rhijn (1973) measured male success in terms of copulation frequency. I measured male success in terms of the frequency of female solicitations at a territory rather than number of copulations per se. The difference between the two approaches is crucial. A female must first solicit before a male can copulate. However, success in stimulating the female to solicit does not guarantee success in copulation. Different factors affect copulation success of a male subsequent to the female's solicitation response, such as the male's response to the soliciting female, distraction by fighting with neighboring males, and interference from, or preoccupation with, satellite males. Since my study was an investigation of female choice, it seemed more realistic to measure male success according to where females indicated their choice by soliciting.

I propose that males and females have different proximate goals on the lek, and this results in different and conflicting interests in satellite males. The female has one immediate goal on the lek, to solicit for copulation. The male has two immediate goals, to stimulate a female to solicit and to copulate. The ultimate goal of fertilization and zygote formation is fairly well guaranteed if the proximate goals are fulfilled.

Resident males benefit from the presence of satellites because they increase the probability that females will solicit at their territories. The goals of resident males complicate their relations with satellite males. On the one hand, resident males profit from satellite males because they help attract and stimulate females. On the other hand, once a female has solicited, the satellite male represents competition to the resident male for copulation with the female, and the resident male no longer benefits from the presence of the satellite male. For the resident male, satellite males are an advantage before a female solicits, and a disadvantage after a female has solicited. In terms of success in stimulating the female to solicit, I conclude that satellite males can benefit resident males when present simultaneously with females. In terms of success in copulation, van Rhijn concluded that satellite males are no longer an advantage to resident males when present simultaneously with females. The two conclusions are not contradictory but rather contribute separate halves of the total picture.

Role of the Male Breeding Plumage

The male breeding plumage is a potential source of stimulation for females while it is erected and expanded in display. The ruffs and tufts may stimulate females by their length and fullness, specific color and pattern, or both. The ruffs and tufts increase in length, and possibly fullness, with age, although the pattern and color do not change (Hogan-Warburg, 1966).

Selous (1907) and Hogan-Warburg (1966) found that males with a high

TABLE 7

Simultaneous Visits by Females and Satellite Males to Each Resident Male's Display Territory

Male	*Percentage of simultaneous visits*	*Number of simultaneous visits*	
		To display territory	*To lek*
	SP Lek 1971		
SB*[1]	30.0	26[2]	87[3]
WS*	22.0	19	87
OT*	21.0	18	87
OSB	13.0	11	87
RM	8.1	7	87
GS	3.5	3	87
CM	2.3	2	87
SP	1.2	1	87
	SP Lek 1972		
OM[4]	60.0	3	5
WS	20.0	1	5
RM	20.0	1	5
SB	0.0		
WZ	0.0		
	TP Lek 1972		
CR*	45.0	13	29
MN	27.8	5	18
ST*	27.6	8	29
OE*	9.1	1	11
DD	6.9	2	29

[1] Asterisks (*) indicate successful resident males with the highest percentages of female solicitations.

[2] The total number of simultaneous visits by females and satellite males to the display territory of the resident male.

[3] The total number of simultaneous visits by females and satellite males to all display territories on the lek during the resident male's tenure on the lek.

[4] This male (OM) received the most female visits. Females did not solicit when satellite males visited this display territory concurrently with female visitations.

degree of success at copulating with females had "optimal" plumage development, while underdeveloped or frayed plumage often characterized unsuccessful males. Neither Selous nor Hogan-Warburg found any correlation between specific color or pattern of nuptial plumage and the degree of preference by females. Hogan-Warburg (1966:193) concluded that the "size and brilliance" of male nuptial plumage influenced female choice rather than color and pattern.

In contrast, van Rhijn (1973:189) suggested that males whose plumage conformed to a "common" color-type on a lek were more successful than males of the "rare" color-type. Van Rhijn (1973:184 and Table 20) classified plumages and hypothesized that males attempt to conform to the common plumage group—dark or light—on a lek. His data analysis suggested that individuals of the "common" plumage group performed more copulations.

My data (Tables 2, 3, and 4) did not confirm van Rhijn's hypothesis. I found no relationship between breeding plumage color or pattern and male success in stimulating female solicitation. I also did not find a consistent correlation between male success and "commonness." When the resident males on my leks were classified by van Rhijn's method, no strong trend was apparent, and in fact "rare" males were slightly more successful than "common" males:

SP Lek 1971
Lek composition 7 dark: 5 light = "dark" lek
Successful males 1 dark: 2 light = "rare" successful

SP Lek 1972
Lek composition 3 dark: 2 light = "dark" lek
Successful males 0 dark: 1 light = "rare" successful

TP Lek 1972
Lek composition 2 dark: 6 light = "light" lek
Successful males 1 dark: 2 light = "common" successful

Conclusions

It appears that several stimuli are available on Ruff leks to influence female choice of partners for copulation. The factors may operate singly or in any combination. The actual combination of factors that produces success in stimulating females to solicit depends on the particular characteristics of the individual males composing a given lek. The factors influencing female choice can thus vary from lek to lek and from day to day on the same lek as physiological and behavioral characteristics of individual males change during the course of the season. A lek may be thought of as a patchwork or mosaic of different stimulus situations. Females probably are influenced to solicit by the optimal stimulus situation, regardless of which component factors create the optimal intensity of stimuli. Thus the factors determining female choice are variable between and within leks, and are relative to the total set of conditions on each individual lek. Whatever combination of factors can provide optimal stimuli for females is potentially successful at eliciting solicitation. On some leks, central territory location alone, high activity levels of resident males alone, or a satellite male alone may create the optimal stimulus. On other leks, a combination of two or three of these factors, or other unknown factors, may be required to produce the optimal stimuli causing females to solicit. Males must compete among themselves to attract the females to their territories and stimulate them to solicit.

This mechanism should insure that females are fertilized by the "best" males without selecting for any one particular male characteristic.

Summary

In this study, I investigated the factors that influence the females' choice of partners for copulation on leks of the Ruff, *Philomachus pugnax.* The study was conducted in Sweden during the 1970, 1971, and 1972 breeding seasons. I developed a standardized method to describe the variation of breeding plumage in all individual males on the leks.

Male success in stimulating females to solicit for copulation was unevenly distributed among the males on each lek. I investigated female preference in relation to potential stimuli that cause females to solicit: location of the display territories of resident males within a lek, display rates of courtship behaviors by resident males, and presence of satellite males on display territories. I found that male success in stimulating females to solicit correlated positively with the centrally located display territory, high display rates of resident males, and the simultaneous presence of satellite males with females on display territories. However, the results varied from one lek to another. Male success correlated with different stimuli in different situations. I concluded that females sought a situation of optimal stimulation composed of some combination of stimuli that males on a given lek were able to produce on their display territories. The situation that provided the female with the optimal set of stimuli, relative to the other stimulus-producing situations on the same lek, was successful in eliciting female solicitation. Female choice of partners for copulation was thus determined by any combination of stimuli on a display territory that optimally stimulated her to solicit at that spot. The successful combination of stimuli influencing female choice of copulation partners varied from lek to lek.

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Whip-poor-will, *Caprimulgus vociferus.* Drawing by William Zimmerman.

THE BREEDING BIOLOGY OF FRIGATEBIRDS —A COMPARATIVE REVIEW

J. BRYAN NELSON

Photographs by the author

Almost everything about frigatebirds is unusual or spectacular. Although all five species now have been studied to some extent, a great many puzzles remain. We are only just beginning to elucidate their breeding biology; and the principal characteristics of frigatebirds have never been drawn together so as to indicate the most unusual features of the group. By emphasizing the implications of the observed facts, I will try to clarify the status and deficiencies of our present knowledge of, in particular, frigatebird eco-ethology. Baldly stated, facts would hardly indicate the relevance of frigatebird studies to comparative seabird biology or reveal the complexities of adaptive systems. Perhaps the basic difference between informed ecological accounts of today and reports of yesteryear is that the latter fail, almost completely, to indicate the interlocking nature of adaptive systems, and instead deal out piecemeal information. Indeed, this could hardly have been otherwise since early investigations were concerned primarily with elucidation of distribution and taxonomy. Breeding biology was treated only at the qualitative, mainly anecdotal, level.

The material in this article comes from my own studies on the Greater Frigatebird (*Fregata minor*) in the Galapagos Islands (December 1963 - July 1964), Andrew's Frigatebird (*F. andrewsi*) on Christmas Island in the Indian Ocean (February - September 1967), and the Greater and Lesser (*F. ariel*) Frigatebirds on Aldabra (January - March 1974). Other primary sources of information include studies by Gibson-Hill (1947), Stonehouse (1963), Diamond (1971, 1972, and 1973), and Schreiber and Ashmole (1970). The basic information on territorial behavior, pair relationships, and breeding success is in practice difficult to obtain and depends on observing individually marked nests and birds for long periods in colonies undisturbed by man. For this reason, much remains to be done.

Characteristics of Frigatebirds

Frigatebirds form a tightly-knit genus (*Fregata*) characterized by 11 primaries, 12 rectrices, small tarsi, small feet with deeply excavated webs and flexible toes, pectinate middle toes, tufted oil gland, and a highly distensible gular pouch in the male.

The five species of frigatebirds include the Magnificent Frigatebird (*Fregata magnificens*), Greater Frigatebird, Lesser Frigatebird, Andrew's Frigatebird, and Ascension Frigatebird (*F. aquila*). Olson (pers. commun.) suspects that the Trinidade population of *ariel* may be specifically distinct, and there have been several attempts to create subspecies of *minor* and *magnificens.*

All frigatebirds are morphologically adapted for a highly specialized type of aerial feeding which underpins their entire breeding ecology and related behavior: in the skeleton, the furcula is fused to the deep keel of the sternum and to the pectoral girdle; the wing loading is lower than that of any seabird; the pectoral muscles are large; the wings are long and pointed with a high aspect ratio; and the tail is long and deeply forked. This extreme lightness and power along with the shape of wing and tail impart great dexterity, considerable speed, and the capability of sustained, economical flight. These capacities are reflected in the frigatebirds' entire foraging and feeding technique. The male *minor* weighs 1,200 grams and has a wing span of approximately 134 centimeters. As Beebe (1924) pointed out, frigatebirds have around 40 percent more wing area than any seabird of comparable weight.

Since the sizes of different species of frigatebirds do not vary greatly (Tables 1 and 2), no major morphological radiation has occurred to adapt the species to obviously different ecological niches. Nevertheless, there is a significant range of bill sizes.

Only small white patches on the underwing (*ariel*) or white on the abdomen (*andrewsi*) break the otherwise entirely black plumage (*magnificens, minor,* and *aquila*) of adult male firgatebirds (Table 3), though there is a variably distinct alar bar in most species. Among the females, only *aquila* has an all-dark plumage. Females of *ariel* and the larger *magnificens* have black throats that distinguish them from those of *minor* with a dirty white or grayish throat. *Andrewsi* also is black throated but with a different pattern on the ventral surface, the white extending onto the underwing (Figure 1 and Table 4).

On Aldabra Island in the Indian Ocean, females of *ariel* show dimorphism in the color of bill and eye-ring (Diamond, 1971), about two-fifths of the population having a blue bill and orbital ring, while in the remainder these unfeathered parts are pink or red. Similar dimorphism occurs in other Indian Ocean populations of female *ariel.* While no female dimorphism has been recorded within a single population of *minor*, geographic variation occurs. In the Galapagos, females have blue bills and pink orbital rings; on Johnston Atoll in the Pacific, at least some females have pink bills and orbital rings; on Aldabra, both bill and orbital ring are always pink; and on Christmas Island in the Indian Ocean, the females have blue-gray bills, a pinkish area at the base of the lower mandible, and a pink orbital ring. Although the adaptive significance of this intriguing situation is completely unknown, Diamond (1971) remarked that these features might subserve reproductive isolation where *ariel* and *minor* are sympatric. In fact, the females of *minor* in the Galapagos, where *ariel* is absent, differ more from *ariel* of Aldabra than do three-fifths of the Aldabra population of *minor.* Similarly, in other parts of the Pacific, both color forms of *ariel* occur together with *minor.* Pink bills are

TABLE 1

Weights and Measurements of Male Frigatebirds

Species	*Mean weight (grams)*	*Mean wing length (mm)*	*Mean culmen length (mm)*	*Mean tail length (mm)*	*Male weight as percent of female*	*Male culmen as percent of female*
Greater Frigatebird (*Fregata minor*)	1,239 (950-1,450) (G)[1] 1,201 (1,000-1,450) (A1)	563 (CI) 608 (A1) 582 (Co)	99.5 (G) 95.6 (CI) 104 (A1) 102 (Co)	379 (CI) 427 (A1) 397 (Co)	76 (G) 84 (A1)	88 (G) 89.5 (CI) 89 (A1) 88 (Co)
Lesser Frigatebird (*F. ariel*)	754 (625-875) (A1)	538 (A1) 534 (Co) 508-554 (M)	80 (A1) 83 (Co) 81-91 (M)	325 (A1) 317 (Co)	88 (A1)[2]	92 (A1) 94 (Co) 94 (M)
Ascension Frigatebird (*F. aquila*)	No information but maximum weight juvenile 1,250; this probably means male weight of around 1,086	562	91.7	384	88 (but agrees with *ariel* because based on *ariel* proportions—juvenile weight: adult weight)	89
Magnificent Frigatebird (*F. magnificens*)	1,500 (read from Figure 3, Diamond, 1973, and not too accurate)	633 (Ca)	112.1 (Ca)	431 (Ca)	96.7[3]	92.6
Andrew's Frigatebird (*F. andrewsi*)	c. 1,400	616	110.5	418 (pers. observ.) 386 (others)	90.3	83.8

[1] Symbols for localities are as follows: G, Galapagos Islands; Al, Aldabra Island; CI Christmas Island, Indian Ocean; Co, Coral Sea; M, Malaya; Ca, Caribbean.

[2] Less sexual dimorphism in size because male already small compared with other frigatebirds.

[3] Less sexual dimorphism because male already large (cf. *ariel* for similar case, but small).

TABLE 2
Weights and Measurements of Female Frigatebirds

Species	*Mean weight (grams)*	*Mean wing length (mm)*	*Mean culmen length (mm)*	*Mean tail length (mm)*
Greater Frigatebird *(Fregata minor)*	1,630 (1,400-1,950) (G)[1,2] 1,427 (1,215-1,640) (Al)	587 (CI) 610 (Al) 607 (Co)	112.5 (G) 106.8 (CI) 117 (Al) 116 (Co)	404 (CI) 386 (Al) 415 (Co.)
Lesser Frigatebird *(F. ariel)*	858 (760-955) (Al)	553 (Al) 547 (Co) 526-580 (M)	87 (Al) 88 (Co) 88-95 (M)	324 (Al) 318 (Co)
Ascension Frigatebird *(F. aquila)*	Calculated from maximum juvenile weight on basis of proportions in *ariel*, gives female weight of 1,238	598	103	405
Magnificent Frigatebird *(F. magnificens)*	1,550[3] Also single specific case of 1,587	650 (Ca)	121 (Ca)	431 (Ca)
Andrew's Frigatebird *(F. andrewsi)*	1,550	648	131.8	468 (pers. observ.) 411 (others)

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[1] Galapagos females particularly large in relation to males in weight but not in other parameters.
[2] Symbols for localities are as follows: G, Galapagos Islands; Al, Aldabra Island; CI, Christmas Island, Indian Ocean; Co, Coral Sea; M, Malaya; Ca, Caribbean.
[3] Less sexual dimorphism because male already large (cf. *ariel* for similar case, but small).

found too, in female *andrewsi* and in most populations of *magnificens;* but in the Caribbean, where *magnificens* is the only frigatebird, the females have a blue bill. Diamond (1971) suggests that the pink bill in *magnificens* and *andrewsi* may be important in maintaining reproductive isolation between these two and *minor,* with which both are sympatric in places. However, *minor* is considerably smaller than the other two; the ventral plumage pattern of the female is highly distinctive in *andrewsi* and *magnificens,* thus identifying the females; while *minor* has highly distinctive display vocalizations, thus distinguishing the males.

Juveniles and immatures can be almost impossible to separate. All except *aquila* have a rust color of variable amount and intensity on the head, neck, and upper breast, particularly strong in *ariel*, and all have a variable black breast band. This plumage later becomes white and then variably mottled with black, according to age and sex. All species have a conspicuous alar bar. Juvenal plumage, apart from some or total loss of the rust color, may be retained for at least 30 months. In all frigatebirds, regardless of regional variation in the size of the race concerned, males are considerably smaller than females. In *minor* of the Galapagos, males averaged 76 percent of the female's weight, whereas on Aldabra this figure was 84 percent. While the males are equally small in both areas, the Galapagos females are larger than the Aldabran ones. This may be because larger eggs have an advantage in the Galapagos, with a significantly harsher environment in which the growth of chicks is slower. Frigatebird eggs in the Galapagos are, in fact, not only considerably larger in absolute terms, but also as a proportion of the female's weight. Similarly in the

Galapagos, female Red-footed Boobies (*Sula sula*) are larger and lay larger eggs than their counterparts on Christmas Island in the Indian Ocean.

Relationships

The suborders Fregatae (frigatebirds) and Phaethontes (tropicbirds) are difficult to place. Although the Pelecaniformes is a diverse group, the suborder Pelecani (pelicans, boobies and gannets, cormorants, and snakebirds) forms a satisfactory core group to which systematists have had difficulty in relating the frigatebirds and tropicbirds. Chandler (1916) related frigatebirds to cormorants, boobies, and pelicans on similarities in feather structure. In some fundamental respects the frigatebirds and tropicbirds differ from each other. Tropicbird chicks are downy at hatching while frigatebirds are naked; tropicbirds have open nostrils while those of frigatebirds are closed. Nevertheless, their primitive osteology and their egg-white proteins indicate affinities of these two groups with each other. The totipalmate foot, gular pouch, and primitive skeletal characters enable systematists to derive both groups from basic pelecaniform stock.

Breeding Distribution

Frigatebirds occur mainly in tropical and sub-tropical blue-water regions of the world's oceans, to some extent replacing each other in the different areas but also showing considerable overlap.

Two of the five species are highly restricted, *andrewsi* to Christmas Island, Indian Ocean (not on Cocos Keeling but possibly a resident in the Anamba-Natuma group, according to Gibson-Hill, 1947), and *aquila* to Ascension Island in the South Atlantic. *Magnificens* occurs mainly along coastal belts and island chains embracing the Caribbean, penetrating southwards along the eastern coast of South America to southern Brazil, crossing the Isthmus of Panama and extending north to Florida and south to the Gulf of Guayaquil along the western seaboard of the Americas. However, except for the Caribbean, it breeds at stations few and far between; and its oceanic-island outposts include only the Galapagos archipelago, Fernando de Noronha, the Tres Marias and Cape Verde Islands.

The remaining two, *minor* and *ariel,* are widespread in the pantropics, particularly the Indian and Pacific Oceans, nesting on only two Atlantic islands,

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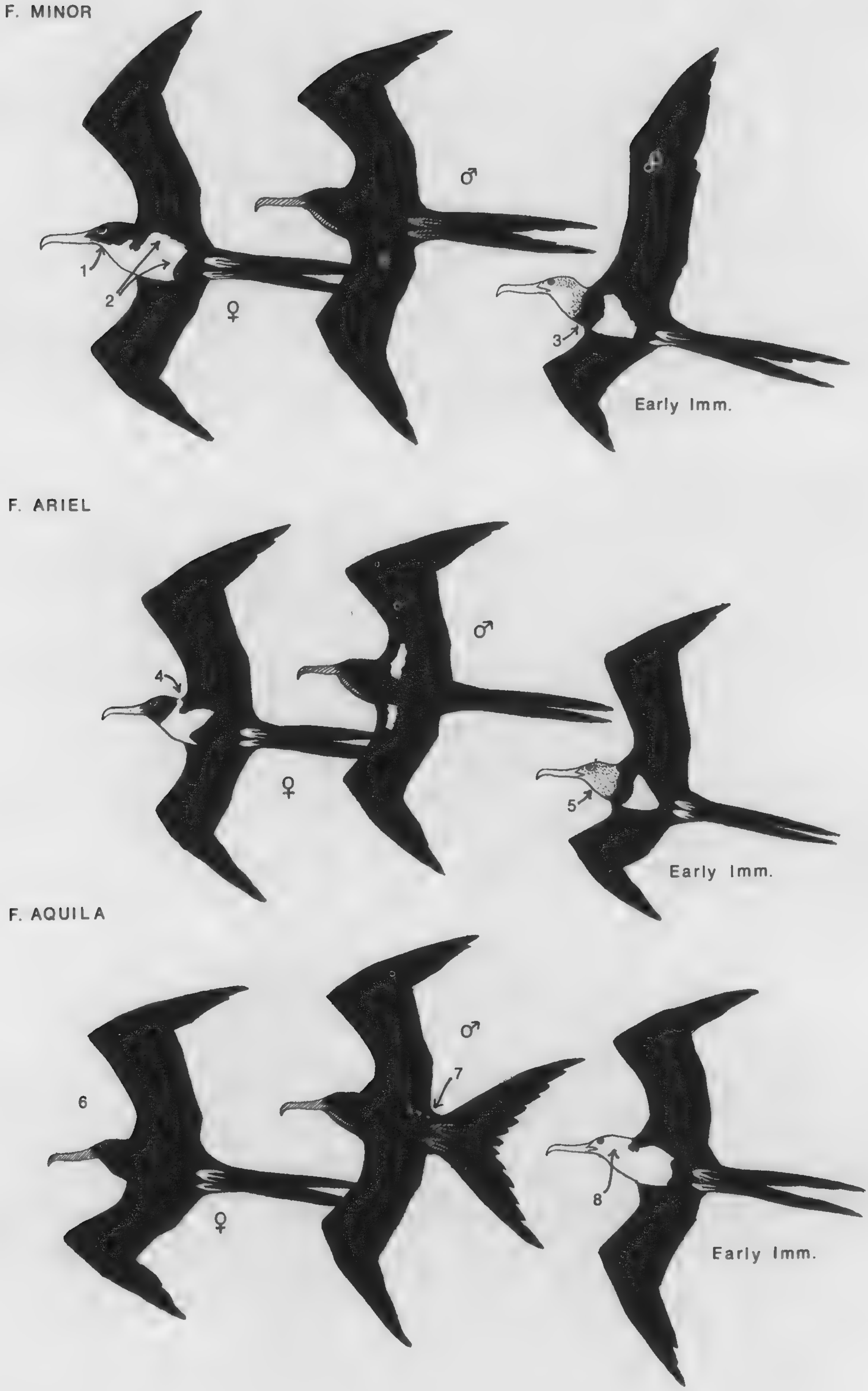
Figure 1. Identifying characters of the frigatebirds of the world. Specific items are as follows: 1. Throat often dusky rather than white. 2. Demarcation between white and black is variable in shape. 3. Black band gradually breaks up and rusty marks disappear while, in immature males, the white ventral surface gradually becomes filled with black. For a time, an immature *minor* can be completely whitish on the head and entire ventral surface, except the vent. On most, perhaps all, of the early immatures of all species, the rusty markings can be solidly massed, variable in shade, and are replaced at variable rates to form white heads. 4. White collar appears to encircle the head. 5. Head may be solid, deep orange, or more streaked. 6. Rusty brown tones in female. 7. Males (young?) may show reticulate pattern of white on the head, or small white patches on the sides of the abdomen. 8. Becomes mottled black as bird matures. Rarely, females may breed with completely white head and abdomen. Immature female *minor* can look much like this, but with more black extending broadly from axillary region onto the sides of the upper breast. 9. This collar may appear somewhat broader, and may be streaked in some (young?) females. 10. Even earlier, this mottling is solidly massed and almost joins in the mid-ventral line. The belly has some pale orange on it. 11. Rusty markings often appear in large streaky masses rather than fine distinct dots. 12. Deep chestnut can be solidly massed here. Drawing by John Busby.


F. MINOR
1
2
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F. AQUILA
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7
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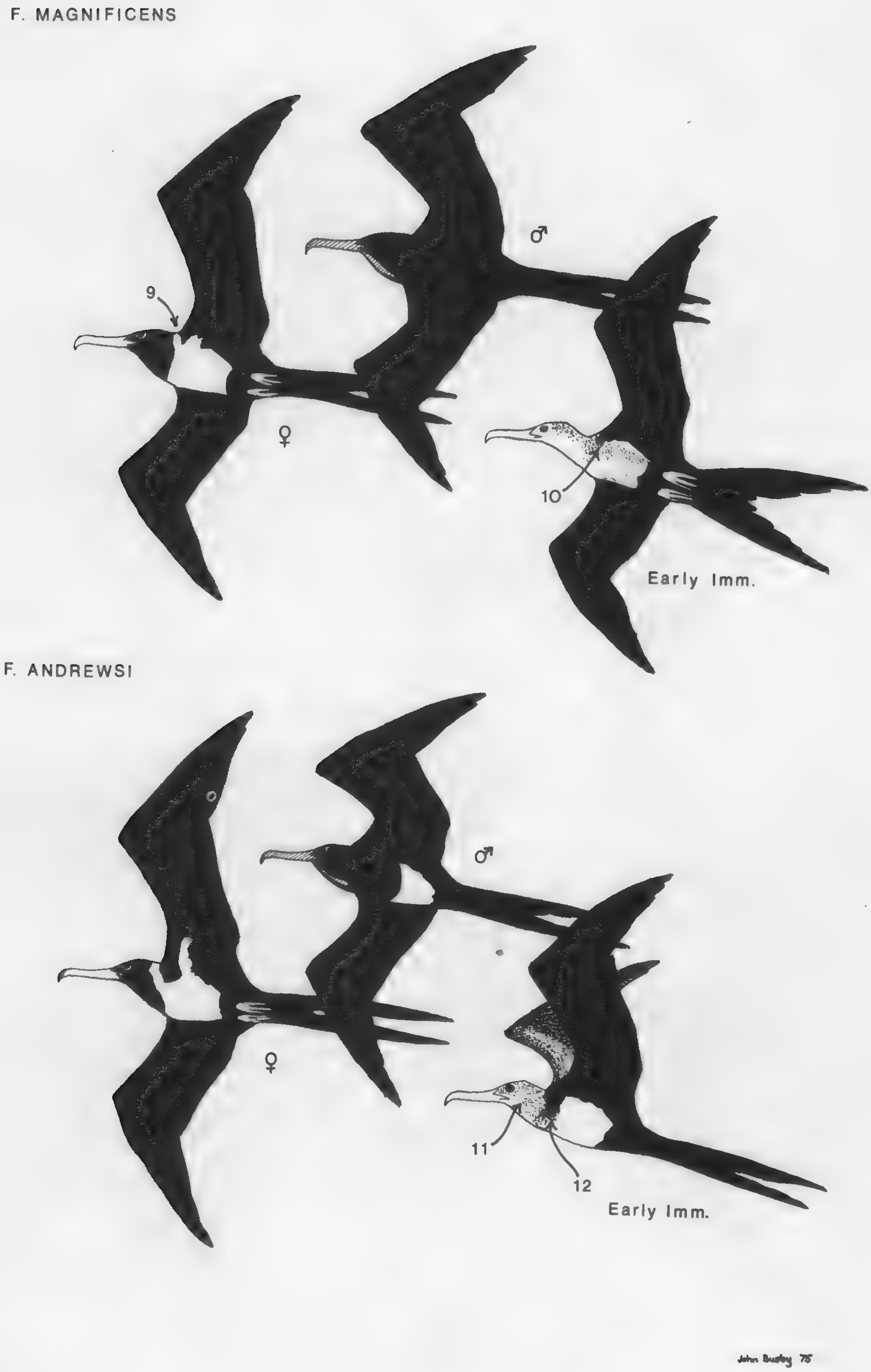
Early Imm.


F. MAGNIFICENS
9
♂
♀
10
Early Imm.
F. ANDREWSI
♂
♀
11
12
Early Imm.
John Busby '75

Trinidade and Martin Vas. *Minor* extends farther north than *ariel* in the Pacific, spanning 50 degrees of latitude between Hawaii (25° N Lat.) and the Pitcairns (25° S). *Ariel's* corresponding limits extend from the Line Islands (5° N Lat.) to the New Hebrides (23° S Lat.). Off Australia, *minor* breeds in the Coral and Banda Seas but *ariel* is more numerous and widespread. The position is, however, partly reversed in the Indian Ocean, where *ariel* extends from the Maldives (5° N Lat.) to the Cargados Carajos and *minor* from there only to Aldabra (9° 25' S Lat.). Diamond (1971) estimates that *minor* and *ariel* overlap on approximately half of the breeding stations on islands where at least one of these species occurs. *Minor* also overlaps with *magnificens* on occasion, as in the Galapagos, but *minor* is a genuine blue-water species, avoiding the muddier coastal areas sometimes tolerated by *magnificens*. *Minor,* but not *ariel,* also overlaps with *andrewsi* on Christmas Island (Indian Ocean).

Breeding Ecology

The vital clue to an understanding of frigatebird breeding biology resides in the link between their highly specialized feeding techniques—snatching flying fish and squid from the surface supplemented by kleptoparasitism, mainly on boobies, conducted mainly in impoverished seas—and the prolongation of their breeding cycle. This, in turn, reduces the frequency of breeding to less than once a year and thus affects the entire web of behavior concerned with territoriality and pair formation (Table 5). Instead of a straightforward annual cycle, a more complex one exists that excludes the normal mechanisms of fidelity to site and mate. These interactions, or etho-ecological adaptations, are based on the dictates of feeding ecology and form the main thread of this article. They may be broadly outlined as follows: (1) Impoverished pelagic habitat and/or specialized feeding techniques lead to (2) slow growth of young

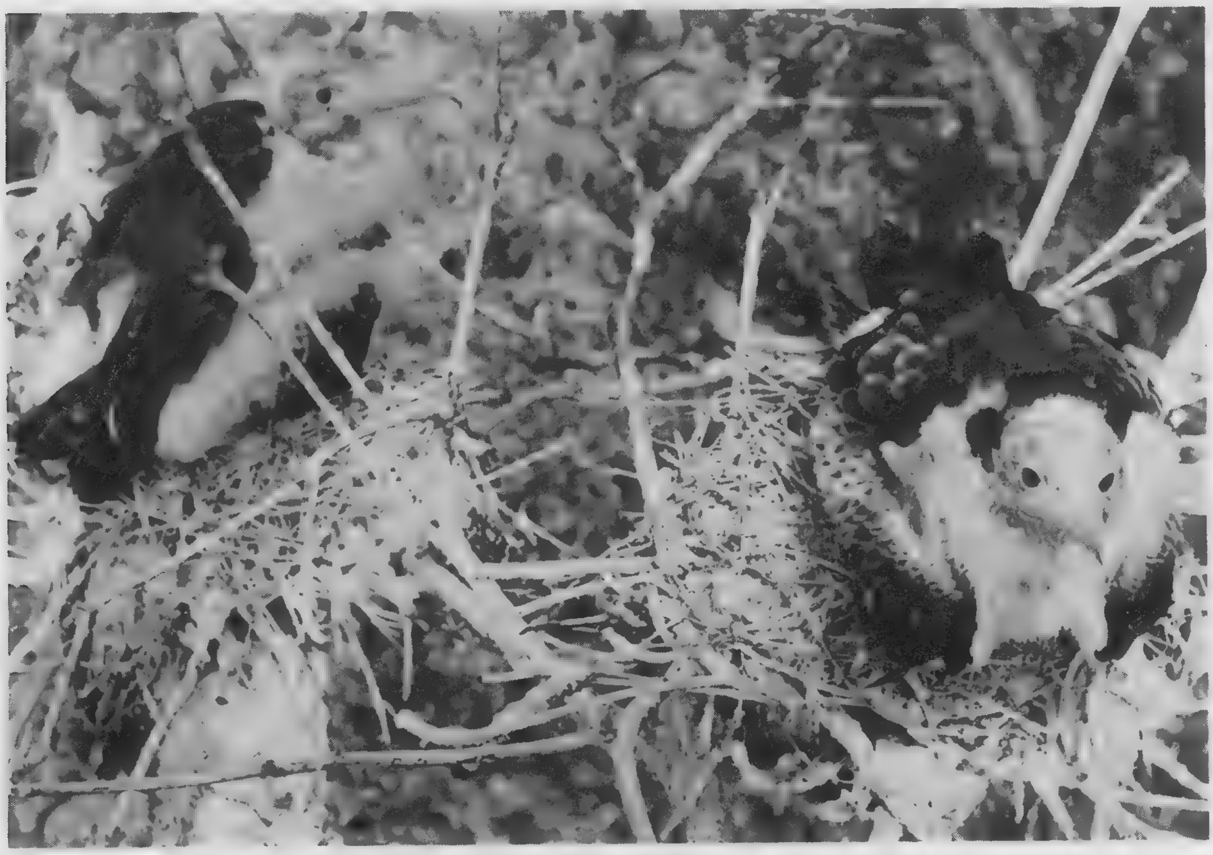


Figure 2. Immature Andrew's Frigatebirds (*Fregata andrewsi*) on Christmas Island, Indian Ocean. Note the proximity of the two nests.

and an extended post-fledging period to enable the acquisition of specialized feeding technique. This necessitates (3) a protracted breeding cycle leading to (4) biennial breeding. This, in turn, causes (5) difficulties in retaining site and mate and thus leads to (6) the abandonment of conventional territorial and pair behavior which (7) affects the nature of behavior patterns that function in these spheres.

Population Size

Minor and *ariel* are probably the most numerous frigatebirds, although one can only guess at the world total, perhaps of the order of one-half to one million pairs. Possibly fewer than 500,000 pairs of *magnificens* exist. *Aquila* numbers from about 8,000 to 10,000 breeding birds (Stonehouse, 1963) and *andrewsi* now comprises less than 1,000 pairs and is declining. It poses a simple conservation problem, for its breeding habitat is safe but the birds themselves are poached by the Malays on Christmas Island (Indian Ocean).

Colony Size and Density

Compared with the immense concentrations of boreal and arctic auks and petrels and the antarctic penguins, or the wideawake fairs of Sooty Terns (*Sterna fuscata*) on some oceanic islands, the frigatebirds and pantropical boobies rarely congregate in vast colonies. Diamond (1975) estimated about 27,000 frigatebirds on Aldabra, including more than 5,000 pairs of *ariel* and about 2,000 pairs of *minor*. This is the largest concentration of frigatebirds ever estimated. Even here, birds occur in different parts of the atoll rather than as one huge group. *Magnificens* numbers some 2,500 breeding pairs on Barbuda and about the same on Isla Desterrada off Yuctan (Palmer, 1962), while Dill (1916) estimated 12,500 individuals on Laysan. At the recently discovered breeding ground of Red-footed Boobies and frigatebirds on Manoek Island (5° 33′ S, 130° 18′ E in the Banda Sea), D. M. Simpson (Royal Naval Bird Watching Society) estimated the frigatebird population at 10,000 (*minor* and *ariel*) in February 1970. As mentioned, *aquila's* colony numbers 8,000 to 10,000 birds.

As in all seabirds, colony size in frigatebirds varies greatly. Some *magnificens* nest solitarily on Tower Island in the Galapagos. Whatever limits colony size, it is not an adaptation to avoid over-exploiting boobies, for frigatebirds obtain most of their food by honest fishing. Even if the ultimate limiting factor is food, it need not operate as a density-dependent check on population size. Nor, usually, are nest sites limiting. Given their slow recruitment, high pre-breeding mortality, and man-caused losses, it is possible that frigatebirds cannot build up their populations to a level at which a density-dependent restriction could operate.

Spatial distribution in colonies probably plays a much more significant role in the breeding biology of frigatebirds than does absolute colony size. All frigatebirds nest in distinct clumps rather than dispersing themselves evenly. Within groups, density varies from a high of around two nests per square meter for *aquila* on some parts of Boatswain Island, Ascension, to 0.06 or less in some groups of *minor* on Tower Island, Galapagos. *Andrewsi* nests in groups of up to twenty in one tree. In all species, birds sometimes nest within touching distance of each other (Figure 2).

There seem to be no species-specific differences in nesting density comparable to those found in boobies. It appears that the existence of nesting groups,

TABLE 3

External Features in the Fregatidae (Adult Males)[1]

Species	*Distribution of white*	*Bill*	*Orbital ring*	*Legs*[2] *and feet*	*Alar bar*
Greater Frigatebird (*Fregata minor*)	None, except occasionally a little on flanks	Slaty blue throughout range; darkest early in breeding season	Dark	Red or flesh	Present; absent in some birds; geographical or seasonal?
Lesser Frigatebird (*F. ariel*)	Wite patch each side of abdominal region, extending onto underwing	Always grayish or blackish; darkest and glossiest early in breeding season	Blackish	Black or reddish brown	Absent (always?)
Ascension Frigatebird (*F. aquila*)	Occasionally show reticulate pattern on ventral surface or small white patches on sides of abdomen	Blue or blackish?	Black	Black	Inconspicuous
Magnificent Frigatebird (*F. magnificens*)	None	Gray, lead-blue or blackish	Black	Blackish	Absent
Andrew's Frigatebird (*F. andrewsi*)	Conspicuous ventral abdominal patch 100 mm (anterior to posterior edge) by 140 mm wide; some males have faint whitish patch in axillary region	Blue or blackish during courtship; some individuals pink when free-flying young	Blackish with small pink area on upper half	Purple marked with brown; soles yellow or flesh	Often conspicuous; broad; pale

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[1] Males of all species have iridescent green gloss on crown (lanceolate feathers) and green or bronze-purple gloss on elongated back feathers and scapulars. The color of this gloss in not a reliable feature for distinguishing between species.

[2] Tarsi feathered.

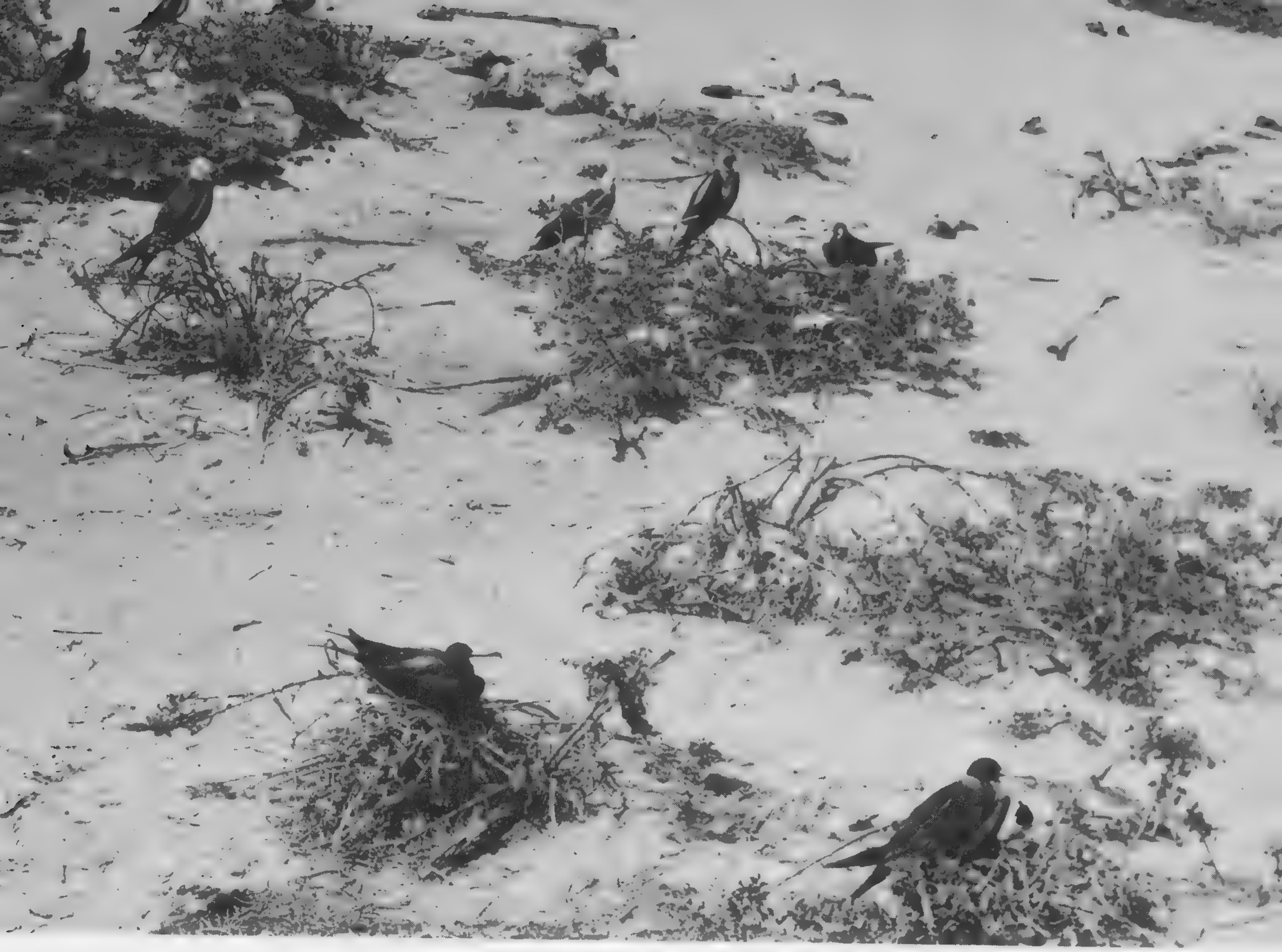

Figure 3. A group of Greater Frigatebirds (*Fregata minor*) on Tower Island, Galapagos, nesting on low scrub.

characteristic of the entire family, stem mainly from the nuclei of displaying males, which are visually most conspicuous when participants are fairly close together. The ragged pattern of nests within clumps or groups could be due to some displaying males failing to acquire partners. If adjacent males do so, extreme proximity of nests results. If display continues after some males of the nucleus have paired, built nests, and acquired eggs, or after new males join a nesting group (as apparently happened in *aquila*), the density of nests may become so extreme that displaying males dislodge eggs or young with their wing movements.

The social stimulation resulting from such communal display causes local synchronization, which may be adaptive (see below). The density within clumps is roughly standard and ensures a degree of synchrony, but the size of clumps and the distance between them is highly variable, having little or no survival value.

Breeding Habitat

Frigatebirds are light, agile, and good perchers. This opens up a wider range of nesting habitat than is available to any other arboreal seabird. Given the right wind direction, a frigatebird can land delicately on a single thin twig a few centimeters or tens of meters above the ground. Landing, not taking off, determines the position and aspect of the nest. Frigatebirds can easily take off so long as they have air space. Wind is needed only for taking off from the ground or exceptionally low sites. However, they cannot land so easily and prefer to do

TABLE 4
External Features in the Fregatidae
(Adult Females[1] and Juveniles)

Species	*Distribution of white*	*Bill*	*Orbital ring*
Greater Frigatebird *(Fregata minor)*	White on abdomen and breast extending onto throat as off-white or grayish (diagnostic)	Varies; blue-gray (G, CI)[4]; pink or red (Al and in Atlantic)	Red throughout range
Lesser Frigatebird *(F. ariel)*	White on abdomen and breast, also flanks, but not extending onto collar, with blackish or chestnut crossing lower hind neck in some	Varies; pink, 60%, blue, 40′ (Al); purplish-gray (Co, and elsewhere; pink or blue (parts of Pacific)	Reddish
Ascension Firgatebird *(F. aquila)*	Occasionally show reticulate pattern of white on ventral surface	(not recorded)	Pale blue
Magnificent Frigatebird *(F. magnificens)*	White on abdomen, flanks, entire breast; black throat; grayish collar around hind neck	Varies; gray-blue (Ca); pink (G)	Blue
Andrew's Frigatebird *(F. andrewsi)*	White on abdomen and breast extending onto underwing, in armpit and around sides of neck in half collar about 35 mm deep; throat black, extending onto upper breast	Pink; extreme tip blueish	Pink

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[1] All adult firgates have brown irises, usually deep brown.

[2] Tarsi feathered.

[3] The situation needs clarifying: females and immatures show much more conspicuous bars than males, but whether *all* males of any species in any area lack it altogether, or whether it often or always appears to some extent due to bleaching and abrasion, is not clear.

[4] Symbols for localities are as follows: G, Galapagos Islands; Al, Aldabra Island; CI, Christmas Island, Indian Ocean; Co, Coral Sea; M, Malaya; Ca, Caribbean.

TABLE 4, continued

Species	*Legs*[2] *and feet*	*Alar bar*	*Characteristics*[4] *of Juvenile*
Greater Frigatebird *(Fregata minor)*	Flesh to reddish	Present, reported absent in Aldabra; possibly seasonal (pre-molt)	Head and neck white variably suffused or streaked rufous; rusty patch upper breast; lower breast blackish extending onto flanks; belly white. Upper parts dark; pale wing bar. Bill largely pale blue (gray).
Lesser Frigatebird *(F. ariel)*	Flesh to reddish	Present	Head and neck mainly rusty; rufous upper breast; lower breast black; belly and flanks white. Mantle brownish, wings blackish; bill pale blueish. Not always distinguishable from *minor* if size fails, though often darker rufous.
Ascension Frigatebird *(F. aquila)*	Pink or coral	Fairly conspicuous	Head, neck, breast, and abdomen white; dark, broad pectoral band, often with gap in midline. Dark above; marked alar bar. Feet and bill pale blue.
Magnificent Frigatebird *(F. magnificens)*	Red, rose, or magenta	Conspicuous	Head and neck white, variably marked rufous; breast and abdomen also buff. Bill gray-blue; feet livid blueish. Alar bar.
Andrew's Frigatebird *(F. andrewsi)*	Flesh pink or pinkish	Present	Head and neck rufous; variable amounts white and rust on breast; blackish pectoral band, white belly. Creamy white alar bar and light belt across shoulders. Bill pale blue.

so into the prevailing wind which means that, as on Aldabra, they often nest on the sheltered side of a mangrove bank (the same consideration determines the northwest facing aspect of the nests of Abbott's Booby, *Sula abbotti*, since the main part of the nesting season occurs during the southeast trades). Their lightness enables them to use fragile sites even on dead branches. Nevertheless, like Red-footed Boobies, frigatebirds occasionally become jammed in forked twigs and perish.

Andrewsi prefers to nest in the sea almond tree *(Terminalia catappa)* never lower than about 10 meters, although whether this is because of human persecution is unclear. Gibson-Hill (1947) stresses the difficulty that *andrewsi* experiences in becoming air-borne and remarks that the only three birds he saw nesting within three meters of the ground all proved unable to take off from this height. *Magnificens*, which is about the same size, nests as low as 0.3 meters on Barbuda and will even nest on bare rocks, cliffs, or tussocks, although it frequently chooses the tops of mangrove thickets. *Minor* and *ariel* are also versatile nesters, using low evergreen and zerophytic shrubs or even cacti and mats of vegetation barely off the ground (Figure 3). On the other hand, I saw *minor* nesting more than 15 meters high in jungle trees on the shore terrace and the inland plateau of Christmas Island (Indian Ocean). They probably prefer mangrove. On Aldabra, *minor* used the flatter tops of the canopy and *ariel*, with its lower wing-loading, chose the sloping sides, so that *ariel* tended to nest lower than *minor* (Diamond, 1971). *Aquila*, which also is small and light, nested on stony ground on the ridges and slopes of the basalt cap of Boatswain Island. This species originally may have nested in trees on the main island, from which it was driven by introduced predators. Where two species nest in the same local area, they usually do not intermingle, although *ariel* and *minor* can be found together in the same small patch of mangrove.

The Nest

All species typically build flimsy, flat platforms of small twigs and other vegetation, that they pick up in a swoop over the ground, wrench – usually in flight – from terminal growth, or steal from Red-footed Boobies and unattended (sometimes even attended) nests of other frigatebirds (Figure 4).

The nest's flatness often endangers the egg when parents change-over at nest-relief. Sometimes the nest disintegrates during the nestling stage, but many yellowish excreta-hardened pads, easily distinguishable from the whitened twigs that are the remnants of a Red-footed Booby's nest, remain until the next breeding cycle and in all species are often selected as nest sites by a new pair. The flimsy nest usually is not the result of a lack of nest material. Possibly, a considerable expenditure of energy would be uneconomical when the bird's lightness and perching ability permit a simple structure, but a better constructed nest would save many eggs.

Eggs

The female *minor* may remain on the nest without a break for up to 10 days before laying. All frigatebirds always lay single-egg clutches. The egg is plain white and thin-shelled, lacking the thick lime layer of sulid eggs. Compared with the eggs of all other pelecaniforms, those of frigatebirds are large, some five to six percent of the female's weight.

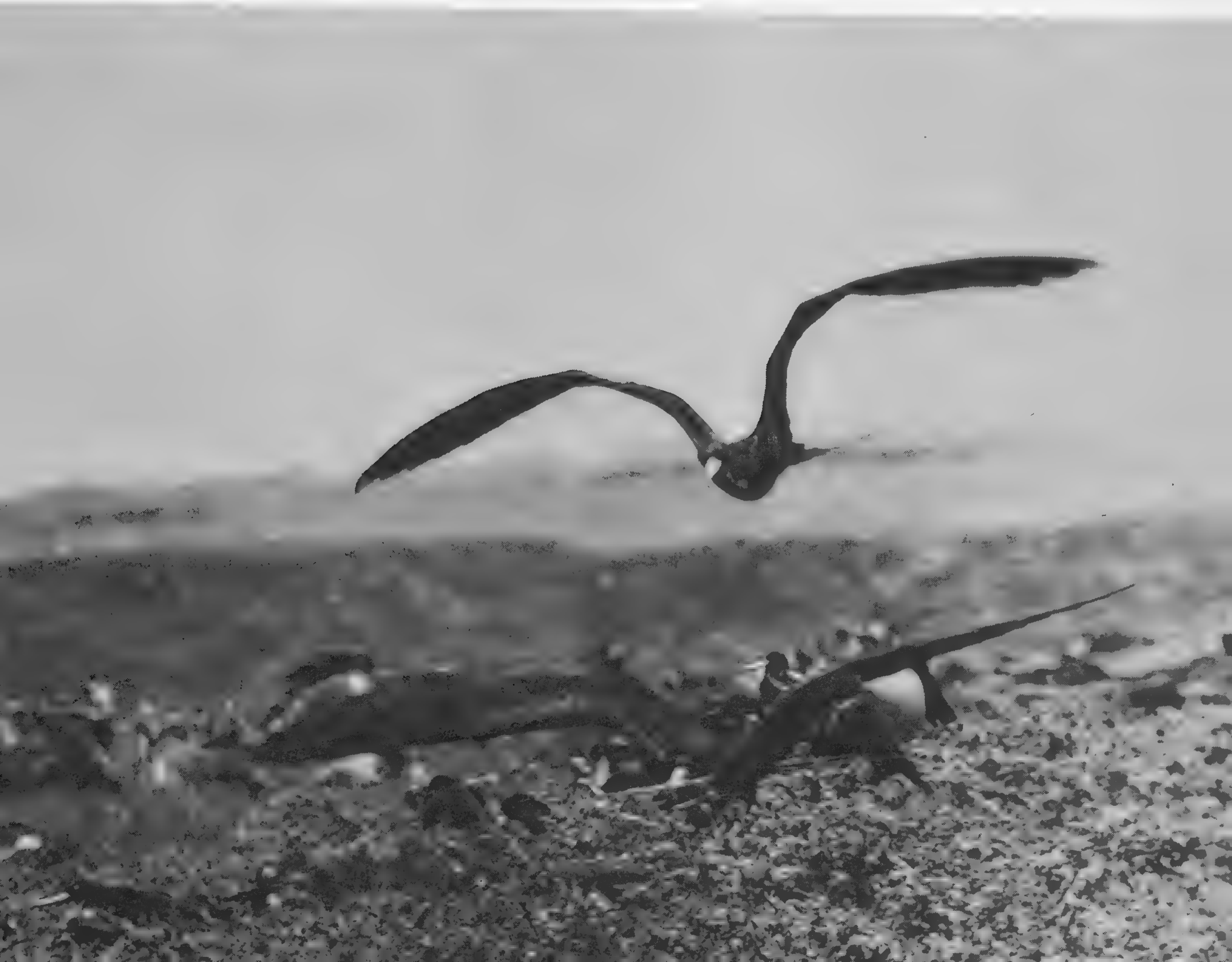
It is not always possible to avoid prolonged starvation in the newly hatched chick, although frigatebirds and several other seabirds substantially shorten their attentive periods and foraging trips as hatching day approaches and the chick begins to call within the egg. Heavier eggs, producing chicks with greater reserves, are adaptive in these circumstances. As mentioned, the female *minor* on the Galapagos is heavier than the Aldabran female, and her egg is larger. This may be an adaptation for the severe conditions of the Galapagos Islands (see Figure 5).

Apparently females usually replaced lost eggs at least once and sometimes more. In 13 cases accurately timed, the replacement averaged 12 days, ranging from 4 to 21 days, and 12 cases less accurately timed averaged 16 days (range 2 to 24). Second replacements averaged 14 days (nine cases) and third replacements 15 days (four cases). Where it was known that more than one pair was involved with the nest, the replacement took much longer (30 days in 14 cases). However, in no case had we marked individuals so that some queries must remain over the matter of replacement laying. It seems particularly questionable that a frigatebird could re-lay in four days or less unless, perhaps, the first egg was lost almost immediately.

Nestlings

Like all pelecaniforms other than tropicbirds, frigatebird nestlings are altricial and naked, except for sparsely distributed tracts of down over a uniformly pale skin that is greenish or bluish in *aquila, magnificens,* and *ariel* and pinkish in *andrewsi* and in *minor* on the Galapagos. The bill, legs, and feet are bluish. By the end of the second week, the white down thinly covers both dorsal and ventral surfaces, and is thicker on the rump. In *andrewsi*, and presumably

Figure 4. A male frigatebird chases another with a stick in its bill. The chasing bird will attempt to steal the stick. Most nest material is pilfered.



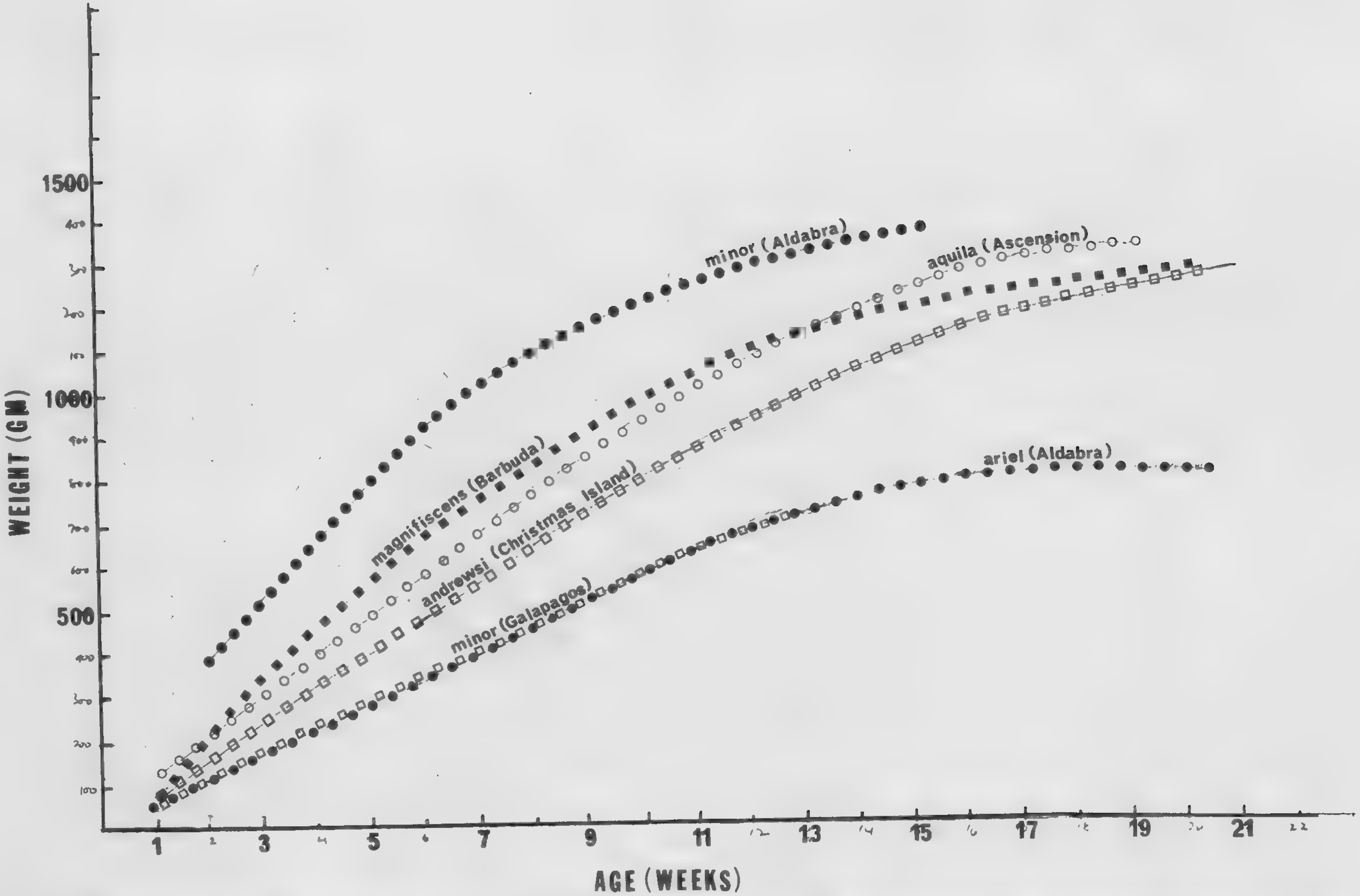


Figure 5. Growth curves for frigatebirds. Data for *aquila* are from Stonehouse (1963); data for *ariel* and *minor* on Aldabra and *magnificens* on Barbuda are from Diamond (1972 and 1975). Data on *andrewsi* and on *minor* from the Galapagos are from Nelson. Note that *minor* in the Galapagos grows far more slowly than it does on Aldabra, despite the fact that adults on the Galapagos weigh more than those living on Aldabra.

other species too, this white or pre-plumule down (Gibson-Hill, 1947) is replaced by a coarser down that is pale smoky gray on the dorsal surface and back and sides of neck. First generation feathers appear on the dorsal and scapular areas in the third week and erupt from their sheaths five or six days after they first appear. The tips of secondary wing feathers appear in the sixth week and primaries a week later, followed by the rectrices. At two months of age (Figure 6) the nestlings are densely covered with down, their backs shielded by black "capes," the scapulars. From then on, the feathers gradually replace the down, mainly between 80 and 100 days on the wings and three weeks later on the head, although traces remain in both areas until about day 140. The body, particularly the belly and flanks, may retain some down until as late as day 180, almost 26 weeks after hatching. Frigatebirds first take to the air when they are six to seven months old in *aquila*; five to six months in *minor* on Aldabra; and around six months for *minor* on the Pacific Ocean Christmas Island, *andrewsi* on Christmas Island in the Indian Ocean, and *magnificens* on Barbuda. The adaptive value of the black scapular cape is unknown but is exactly paralleled in Abbott's Booby and probably relates to temperature regulation, for it appears at about the time when parents stop brooding their nestlings.

Diamond (1973) recorded an interesting difference between male and female nestlings of *magnificens* on Barbuda; small-billed nestlings, presumed males, had browner wing bars than larger billed birds. Of 19 nestlings, nine had brown bars and a mean bill length of 105.8 millimeters, while 10 had whiter wing bars and a bill length of 120.9 mm, a highly significant correlation. Using wing-bar color as a criterion of sex gave a male:female ratio of 1:1.8. Diamond (1973) interprets this unexpected preponderance of females as possibly the basis of the system whereby males breed twice as often as females (see Page 000).

Duration of Dependency

In all frigatebirds, the chicks grow very slowly (Figure 5). There are, however, slight differences between species. On Aldabra, *minor* grows considerably faster than *ariel*, possibly as a result of differences in the feeding ecology of the adults. But in all cases, it takes at least five months from hatching to fledging, and in most cases, six or seven. The post-fledging period, during which the adults continue to feed the free-flying young, is even longer: six to ten months or more for *minor* in the Galapagos and up to 14 months or more on Christmas Island in the Pacific (Schreiber and Ashmole, 1970); at least nine months for *andrewsi* on Christmas Island and probably 5 to 12 months for *ariel* and *minor* on Aldabra. The duration of both the fledging and post-fledging period is so long because of the feeding behavior of frigatebirds. They can catch prey only by surface dipping or aerial snatching and cannot exploit the deeper layers available to boobies, tropicbirds, cormorants, and even pelicans. Moreover, they appear not to bother much with the small fry that terns pursue. Combined with the paucity of food that often characterizes its feeding areas, this imposes much lengthier foraging trips than are necessary for boobies, terns, tropicbirds, and pelicans, and often yields small returns. An albatross or penguin may be away for equally long periods, but because of the different system of food storage and greater probability of encountering good feeding, these birds rarely, if ever, return empty-handed. The frigatebird's lightness and tropical distribution endow the species with low energy requirements and permit a low intake of food relative, for example, to a Gannet, *Sula* [*Morus*] *bassana*.

Nestlings and fledglings are thus provisioned by parents highly adapted to scraping for a specialized living in impoverished areas. Nestlings get relatively

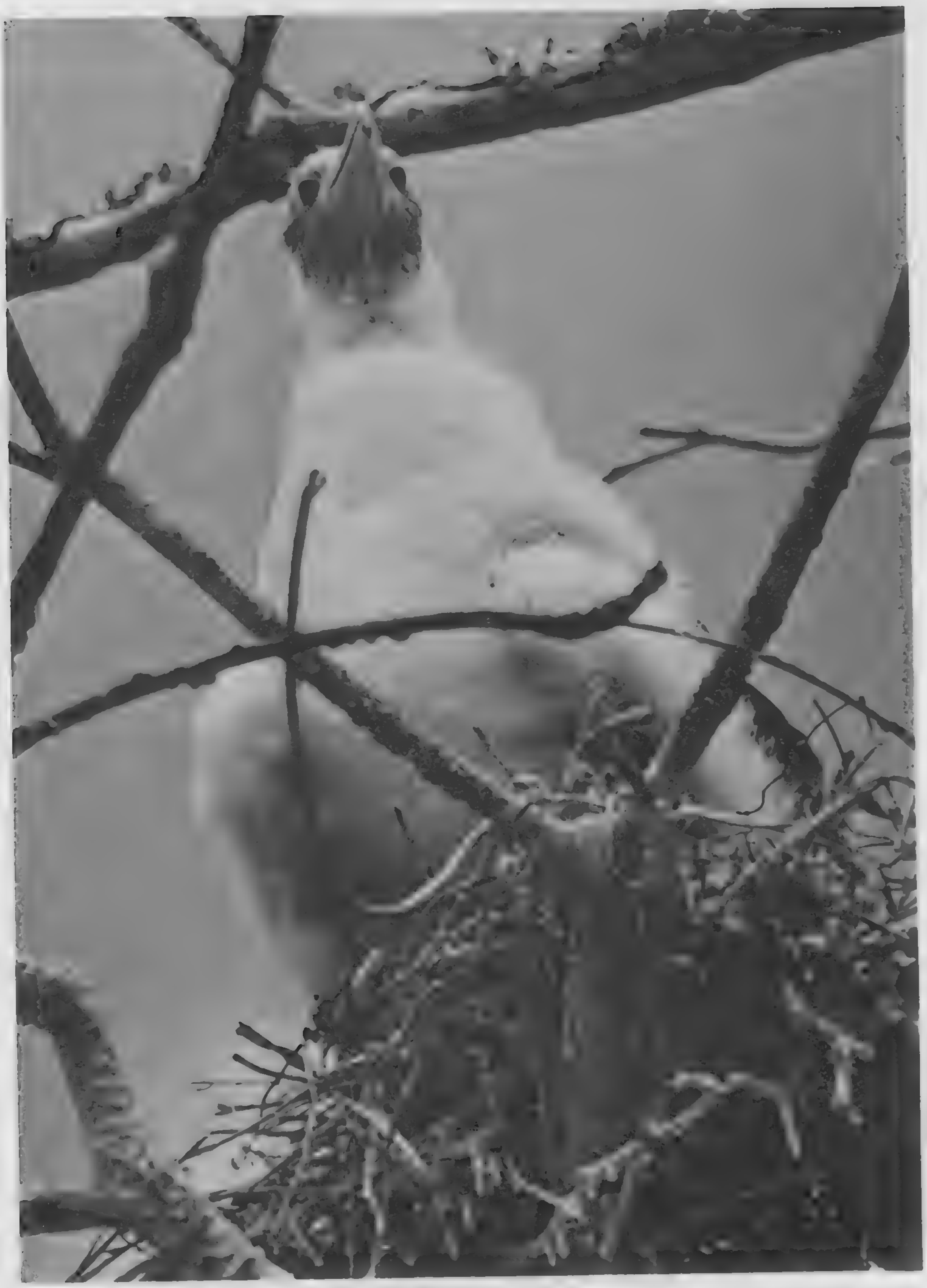


Figure 6. Young Andrew's Frigatebird (*Fregata andrewsi*) on Christmas Island, Indian Ocean.

little food relatively infrequently, and so they grow slowly. Frigatebirds are highly adapted to food shortages because they have to be. Their distribution and feeding techniques make shortages inevitable, but correspondingly, the frigatebirds are adapted to cope. Predictably, extreme adaptations have evolved to meet extreme conditions, and where local ones are favorable, as in *andrewsi*, and in *magnificens* of Barbuda, the pattern may be significantly modified. Thus, it appears that *magnificens* on Barbuda may have evolved a unique division of labor whereby only the female feeds the fledged young and the male is released to begin a new breeding attempt (Diamond, 1973).

Often, however, it requires much of the adult's energy to cope even with one slow-growing, starvation-resistant chick; and when this one bird fledges, an uphill struggle is assured, since there is no seasonal flush of food to exploit, as newly independent King (*Aptenodytes patagonica*) and Emperor (*A. forsteri*) Penguins do with their euphasiids. Furthermore, the specialized feeding techniques of frigatebirds take time to acquire. The only evolutionary answer is a lengthy post-fledging dependence on the parents. Even after several months of parental subsidy, the juvenile *minor* (or, in fact, a second-year bird as it may then be) is considerably lighter than an adult (Table 6) and may yet starve when left entirely on its own.

The scale and consistency of post-fledging feeding in the Fregatidae is remarkable, exceeding the normal dependency period of tropical boobies, specialized though they are.

Breeding Success

At any frigatebird colony the proportion of adults that attempt to breed is almost impossible to determine. Even the sex ratio may be distinctly unequal, as in *minor* on Aldabra, where there seem to be more males than females. It is also difficult to estimate the proportion of displaying males that eventually acquire a female and build a nest. On Tower Island, we marked 230 sites of displaying males, from which 226 pairs, 212 nests, and 206 eggs resulted. This appears to be an extremely high success rate but all frigatebirds have a very low breeding success (Table 5), defined as chicks fledged from eggs laid. It would be more correct to define it as young reared to independence from eggs laid but this is impracticable with existing data. They are extremely prone to lose eggs and chicks, and mortality continues even among free-flying but dependent young.

In all species of frigatebirds, probably 15 to 25 percent of the eggs laid yield fledged young. This compares with 60 to 80 percent in the sulids. Breeding success in frigatebirds varies considerably, however, even within the same population. Certain groups of *andrewsi* on Christmas Island (Indian Ocean) had achieved a breeding success of 60 percent by the time the nestlings were half grown, when my observations stopped. A group of *aquila* on Ascension achieved 48 percent and on Aldabra, one group of 48 nests achieved an estimated 83 percent breeding success. However, in other groups in these same colonies, only 20, 14, and 13 percent, respectively, produced fledged young; the Aldabra groups averaging 13 percent comprised 448 nests.

Although the pattern of egg and chick loss may not be everywhere the same, it probably depends on the same social and ecological factors. These fall into four categories: (1) disturbance by conspecifics; (2) starvation; (3) predation; and (4) accidental. On Tower Island, gross disruption was caused by unmated males settling on or near nests occupied by paired, incubating, or brooding females and unguarded chicks (Figure 7). Some actual display nuclei sprang up amid incubating birds. Other males were sub-adult and probably not ready to breed.

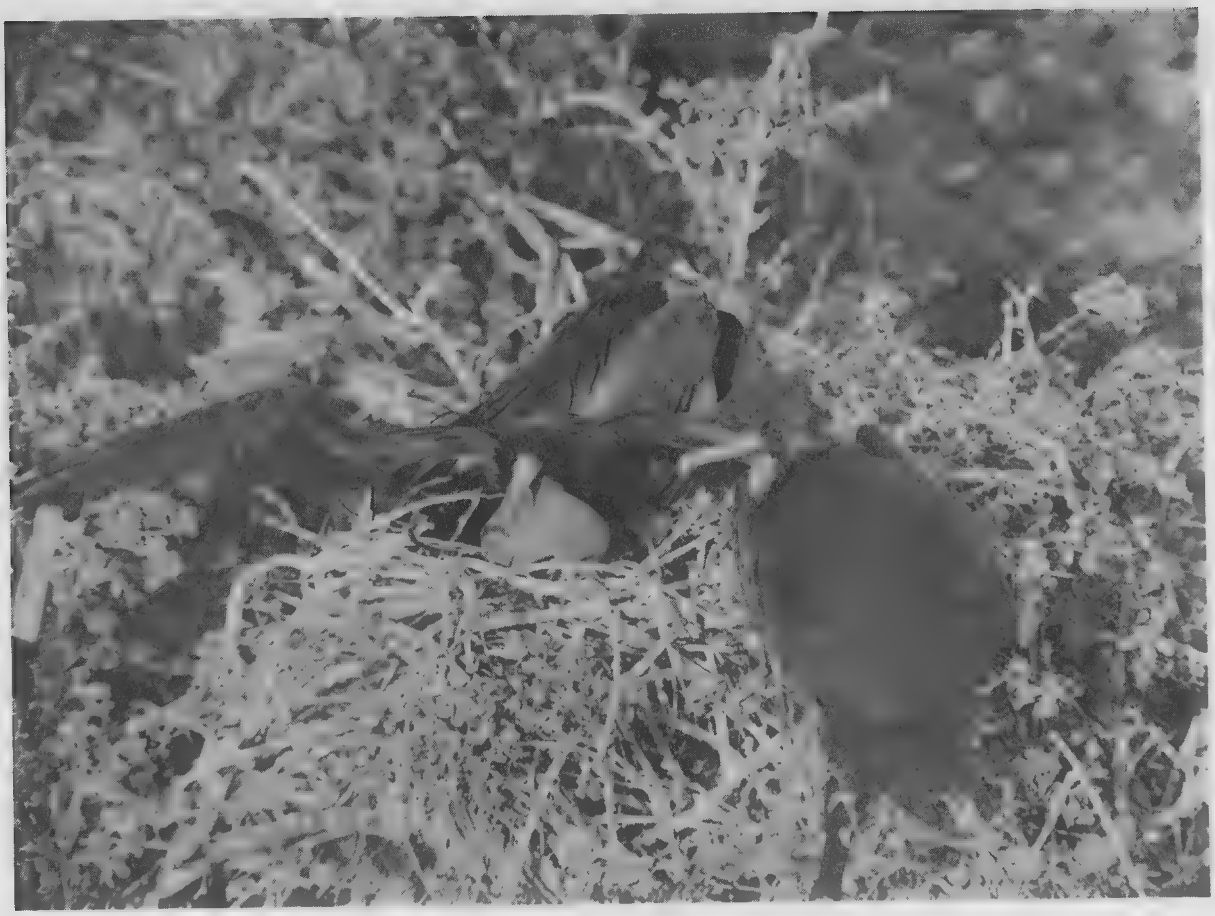


Figure 7. Three Greater Frigatebirds (*Fregata minor*) on Tower Island, Galapagos. On this island, disruption of nests occurred frequently as unmated males landed near active nests. This scene appears to be a typical case of interference by several males at a single nest.

The destruction was spectacular. Eggs were strewn beneath nests; sometimes two, or even three, successively laid eggs were dislodged from the same nest. Unattended young were actually attacked, usually evicted from the nest, and sometimes killed. Evicted birds usually perished on the ground. In the two study groups, 63.1 and 65.1 percent of all eggs laid were lost, and 52 and 55 percent of the nestlings had been lost by the time we left, giving an overall breeding success of no more than 15 percent. Of these chick losses, other frigatebirds caused 43.8 percent and were suspected to have been the cause of an additional 29.8 percent. Owls killed 12.2 percent of the nestlings, and the remainder disappeared by unknown circumstances soon after hatching. On Aldabra, Diamond (1971) also recorded the tendency of males to attempt to pilfer nest materials, sometimes from nests occupied at the time. And he specifically remarked on the high proportion of small young that disappeared.

Diamond (1971) also noted a significant imbalance in the sex ratio, with many spare males. That roughly the same unexpected phenomenon should occur in two populations with such different ecological circumstances suggests that it may be typical of the species. Male *minor* definitely continue to feed free-flying juveniles for several months, so that the extra males cannot be ones that have been released from breeding duties before their partners; yet males, whether "extra" or not, appear to be the key to the situation, for they cause most of the disruption.

Loss of eggs and small nestlings was extremely high in *aquila* on Ascension. One group of 166 nests lost 60 percent of its eggs, and 50 percent of all nestlings died in the first three weeks. Again, interference by conspecifics was almost certainly the main cause. Little human disturbance occurred and no predators existed. Interestingly, the highest breeding success appeared in the low density groups and in those birds breeding early or late in the season—in other words, when there were fewer potentially disrupting males around. Thus the findings in the Galapagos and on Ascension raise intriguing problems concerned with the adaptive value of nesting in dense and relatively synchronized groups. Some earlier observers (such as Dill, 1916) also noted massive predation of eggs and young by conspecifics; but one is unable to ascertain how much of the destruction was caused by human interference.

I recorded starvation in a few cases in *minor* on Tower Island but of greater importance was intraspecific interference and predation (Nelson, 1968). Short-eared Owls (*Asio flammeus galapagoensis*) preyed upon young frigatebirds soon after the parents had stopped guarding them around 35 days but while they still remained highly vulnerable. As with attacks by unoccupied males, the depredations of owls could have been thwarted by prolonged guarding by parents; but presumably both parents were needed for food gathering. Accidents that involved eggs and young falling out of nests occurred rather commonly. Beck (in Murphy, 1936) long ago noted the frigatebirds' habit of dislodging its eggs. But it seems likely that intruding adults often dislodged them. My field notebook contains many accounts of interference and I wrote "frigates seem beautifully adapted for sabotaging their own breeding effort." Interference is discussed further on page 144.

Mortality Following Independence

There is no direct estimate of mortality in the first year of independence. Circumstantial evidence suggests that losses are relatively light, since frigatebirds experience unusually low fledging success but then continue to feed their free-flying young for many months. Probably no more than 20 to 30 percent of frigatebirds die during their first year of independence, which is a low figure compared with many seabirds. Under the stress of harsh climatic conditions or other circumstances, the figure may be higher, for it was clear that on Tower Island in 1964 several newly independent *minor* starved.

Adult mortality is likely to be less than that of tropical sulids, since the recruitment rate is lower. Adult boobies have a mortality rate of considerably less than 10 percent per year, so that a figure of around four percent for frigatebirds, giving a life expectancy of 25.6 years, seems reasonable. Since this is a mean figure, some individuals probably achieve an age of 40 or 50 years, as some albatrosses are known to do. With this life expectancy, frigatebirds can maintain numbers even with the very low breeding success of 20 percent or less. Conversely, seabirds with a high breeding success, such as the Atlantic Gannet with 80 percent, suffer heavy mortality immediately after achieving independence. In its own framework, the apparently wasteful loss of eggs and young in frigatebirds is relatively unimportant.

The slow growth and biennial breeding, with consequent dislocation of normal systems of territorial behavior and mate fidelity, lead to some of the social disruption already described. But, for this price, frigatebirds gain the occupancy of a niche in a globally extensive environment. Frigatebirds form a group as successful as sulids or albatrosses. Making a specific comparison, there are many times more *minor* in the world than there are Atlantic Gannets, despite the social order and extraordinarily high breeding success of the latter compared with the social disorder and low success of the frigatebird.

TABLE 5

Aspects of Comparative Ecology in the Fregatidae

Species and area	*Breeding periodicity (successful birds)*	*Main laying period*	*Nesting habitat*	*Egg weight (grams)*	
				Absolute weight	*Percentage of female body weight*
Fregata minor (Galapagos, Tower)	Presumed biennial: under special circumstances could be 18 months	February-April	Low bushes, mainly at height of 3-6 feet	85 (69-96)	5.2
(Aldabra)	Not known	June-December; peak, August/September	Mangroves, 5-20 feet above high water level	81 (66-90) ?	5.7
F. aquila (Ascension)	Annual or slightly less than annual[3]	September-November	Rocky ground	75.8 (47-92)	About 6.0
F. ariel (Aldabra)	Not known; suspected biennial	August-November; peak, September/October	Mangroves, 3-20 feet above high water level; more often on side than top	59 (only one weighed	6.9
F. magnificens (Barbuda)	Female biennial (?) Male annual (?)[5]	October-January	Low mangrove (*Avicennia* sp.)	Not recorded	—
F. andrewsi (Christmas Island)	Biennial	April-June	Trees, usually at height of 15 or more meters	82 (78-88)	5.3

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[1] Percentage of well-grown of fledged young compared to number of eggs laid.

[2] Many chicks only half grown when numbers ceased; 15 percent or less would be a truer figure for breeding success.

[3] This tentative conclusion (Stonehouse and Stonehouse, 1963) may be invalid since it was not known that the birds concerned had actually bred successfully.

[4] Chicks fly ". . . during their 6th or 7th month." (Stonehouse and Stonehouse, 1963)

[5] Diamond says, ". . . if moult is restricted entirely to the non-breeding period Frigatebirds could not breed more often than once every two years. My data on moult suggests this is so."

TABLE 5, continued
Aspects of Comparative Ecology in the Fregatidae

Incubation period	*Fledging period*	*Duration of post-fledging feeding*	*Role of sexes in incubation and feeding*	*Mean age when young first left unattended*	*Breeding success*[1]
55 days	24 weeks (estimate)	Up to 9 or more months (shortest period unknown)	Shared role in all capacities	31 days (20-39)	Group 1: 19%[2] (62 nests) Group 2: 19% (277 nests)
Not recorded	20-24 weeks (estimate)	At least 4 months, up to at least 14 months on Christmas Island (Pacific)	Females apparently give more feedings to young in nest	Sometimes as early as about 35 days	10-83% in different groups: 10; 13; 13; 23; 41; 44; 67; 83
44 days	20-24 weeks[4]	Not recorded	Shared role in all capacities	About 30-40 days (sometimes earlier)	Mixed *minor/ariel*, averages about 15-20%; one group achieved 48%; some samplings (not groups) had as little as 6% success
Not re-recorded; probably 44-46 days	About 20 weeks	At least 4 months; probably longer	Shared role in all capacities	Sometimes as early as about 35 days	As above
Not recorded; 50 days used by Diamond (1973) but probably more	About 24 weeks	More than 4 months	Shared role until chick about 3 months, then female apparently completes the rearing process alone	About 40 days (sometimes earlier)	Not recorded
About 54 days	24 weeks	Up to 9 or 10 months	Shared role in all capacities	About 45 days	Overall, about 30% at most; certain groups probably more than 50%, others less than 20%

Breeding Regimes

No frigatebird, so far as is known, has a simple annual breeding cycle, but we are still far from understanding exactly what is typical breeding periodicity for each species and how it varies regionally. We need to know: (1) how long a complete breeding cycle takes; (2) the length of the intervening time period; (3) what happens to birds that fail to breed and those that fail at breeding attempts; and (4) the effects on breeding frequency of the protracted laying period.

(1) On the Galapagos and Christmas Island in the Pacific, *minor* takes over a year to complete a cycle: two to four weeks for display and pair formation; eight weeks for incubation; about 20 to 24 weeks for growth of the nestling; and up to a year of parental feeding of the free-flying young. If one assumes that, on the average, parents feed their flying young for six months, the breeding cycle lasts for at least 14 months.

(2) Apparently, frigatebirds molt only when not breeding. Neither Diamond (1971) nor I found any breeding *ariel* or *minor* with molting wing or tail feathers. Chasen (1933) mentions that *andrewsi* molts from August on. It seems likely that these were birds that had just finished feeding free-flying juveniles that hatched the previous year. Gibson-Hill (1947) stated that this species molts between the end of November and early February. The above authors were not aware that *andrewsi* feeds its juveniles until at least July of the year after fledging (pers. observ.). Schreiber and Ashmole (1970) recorded a major molt in *minor* on Christmas Island (Pacific) that lasted from mid-August into November. Frigatebirds thus differ from sulids, and may require several months to complete their molt, which apparently is an extensive one. Harris (1969) suggested that for several Galapagos seabirds, the time required for molt prevents continuous breeding in a relatively seasonless environment. This may be true for frigatebirds. Even though boobies can molt and still gather enough food for their young, frigatebirds may be unable to do so.

(3) Some 80 percent of a frigatebird population fail in their breeding attempt. Some re-lay after about 14 days; others disappear from the colony. Late in the breeding cycle, all breeding *minor* whose nests failed disappeared from the Tower Island (Galapagos) colony. Presumably, they simply wait until the next season and try again, suggesting that at least 80 percent of the population attempts to breed each year.

(4) Not only does the display period last five or six months, flaring up at intervals as new influxes of males arrive (*minor* on Tower Island, Galapagos), but different islands—and even different parts of an island or atoll (*ariel* on Aldabra, Indian Ocean)—are somewhat out of phase with each other. Thus, it is theoretically possible, as Harris (1969) pointed out, for successful breeders to move between colonies in the same island group or on the same island and breed at 18-month intervals. The lack of fidelity to both nest sites and between mates that this suggestion implies is consistent with my behavioral evidence. Also, the distribution of *minor* on Aldabra in 1974 differed markedly from that between 1967 and 1969. The possibility of movement between colonies cannot, therefore, be totally discounted.

The issue is thus between an 18-month and a biennial cycle. On the grounds that (1) at least some individuals feed their free-flying young for so long that they could not breed more than once in two years, (2) that 18 months is an improbably short average, and (3) that a lengthy rest and molting period seems likely, I believe that *minor* must be a biennial breeder. *Andrewsi,* too, is biennial because its laying period is restricted and the feeding period of fledglings lengthy. I recorded in July both males and females feeding free-flying young that had hatched more than a year before. *Aquila* lays in all months although it peaks between September and November and, like the Ascension Brown Booby, *Sula leucogaster* (Simmons, 1970), could have an unusually short cycle. *Magnificens* is perhaps most intriguing of all. Diamond's (1973) observations on Barbuda indicate an unusually disparate sex role in feeding young, females alone caring for them after the age of about three months, thus allowing males to breed annually, while females breed biennially. This unique situation, if confirmed and if species specific, could be correlated with the tendency of *magnificens* to occur in richer coastal feeding areas than the oceanic *aquila, minor,* and *ariel.* This differential sex role in parental care does not apply to *andrewsi* since I saw males of this species feed free-flying young at least eight months old.

The long breeding cycle in frigatebirds is due to their specialized feeding technique which takes a long time to acquire. Other tropical seabirds of similar biomass and food preferences, notably the boobies (with the exception of Abbott's Booby), breed annually or nearly so. It is probably no coincidence that the two boobies facing comparable difficulties, the Galapagos population of *Sula sula* and the aberrant *Sula abbotti,* also possess by far the longest periods of post-fledging feeding, approaching that of frigatebirds. All other seabirds, even those with long nestling periods, become independent either immediately after fledging or within a month or two. As mentioned, probably 80 percent of any frigatebird population attempts to breed every year. In some areas, an aseasonal environment apparently offers no predictable advantages favoring laying in any particular period. Under these conditions, a heterogeneous assemblage of failed and successful breeders and of young birds breeding for the first time inevitably shows a protracted spread. Laying in any one colony commonly occurs over a period of five or six months (*minor* in the Galapagos; *minor* and *ariel* on Aldabra; *magnificens* on Barbuda). In some cases, as in *magnificens* in the Galapagos, laying occurs all year. *Andrewsi,* with the most restricted period, lays on Christmas Island between April and June, while *minor* lays between March and May. In similarly seasonal areas, especially monsoon, other species—for example, *ariel* and *minor* on Aldabra—have fairly well-defined laying periods, mainly August to October (Diamond, 1971, and pers. observ.).

On Ascension, where *aquila* lays over a longer period (Stonehouse, 1963), major peaks occur between periods in which females lay few eggs. There were courting and incubating birds throughout the year but fewest between February and May (1958). In May courtship increased. The number of new eggs increased slowly in June and July and rapidly from late August to a peak in October. The largest number of eggs (1,826) was recorded on October 13th.

The degree of timing that does occur in an apparently largely aseasonal environment, such as Tower Island, is difficult to explain in adaptive terms. Since the parents feed their young for at least a year, and food is highly unpredictable throughout that period, the timing would appear to make little difference to a frigatebird's chances of survival; but it would require critical observations over several breeding cycles to determine this.

Nor are the social advantages clear. On the basis of evidence for several vertebrates, one assumes that breeding synchrony reduces the likelihood of intraspecific interference. If all birds in a group incubate during a given period, there is less chance of disturbance than if incubation, courtship, and feeding young proceed simultaneously. However, prevention of disturbance is precisely what frigatebirds so obviously fail to achieve. As already emphasized, most of their losses are due to males actually landing on nests occupied by incubating

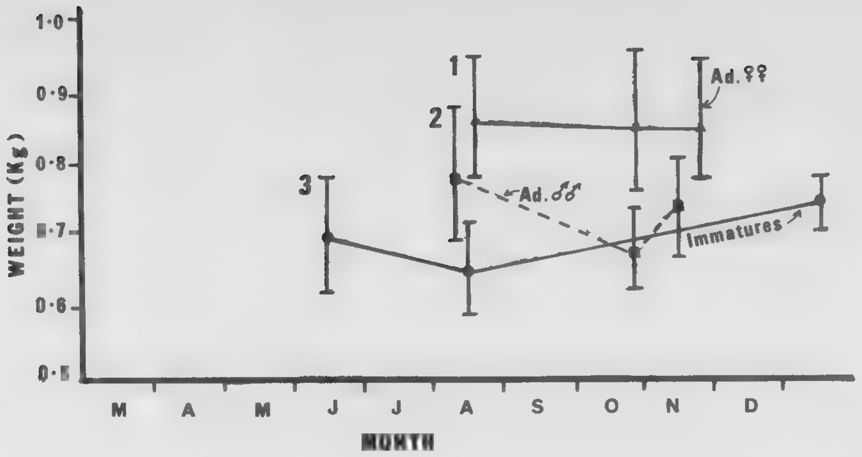


Figure 8. Seasonal changes in the weights of the Lesser Frigatebird (*Fregata ariel*) on Aldabra Atoll, Indian Ocean. The groups considered are adult females (1), adult males (2), and immatures (3). Data are taken from Diamond (1971).

females and attempting to court, rape, or take over the nest. Display nuclei, attracted to the vicinity of nesting groups, often (as in *aquila* on Ascension) disrupt incubating birds, even if by accident. On Aldabra, too, substantial loss of eggs and young resulted from interference by conspecifics. Even in the densest areas of Ascension, where the wings of courting birds tumbled eggs and nestlings from adjacent nests, such damage could not have ensued had all pairs been courting, rather than some courting while others incubated or cared for young. Yet, should it not be assumed that all this social activity, disruptive though it is, has some adaptive value?

Birds attempting to breed presumably comprise individuals that failed at various stages in their last attempt, as well as successful breeders. Small groups are often very closely synchronized, but they are often invaded by a new wave of displaying males. For at least half the year, a colony always consists of a mixture of stages. At the point when pairs from the first wave of displaying males have hatched their eggs, the colony contains nuclei of displaying males, pairs building nests, pairs incubating, small young, dependent free-flying young, and immatures and subadults of both sexes. Later, when unsuccessful breeders disperse, display ceases, and young become almost fully grown, frigatebird colonies are in their most uniform phase: adults are away foraging, the previous crop of young have either dispersed or are absent most of the time, and most of the current immatures have dispersed.

The happenings described above may suggest intrinsic regulation of numbers or population homeostasis (Wynne-Edwards, 1962). Although breeding success is lowered, there is no reason even to suspect that the losses are in any way proportional to fluctuating environmental conditions, which are usually unpredictable. If long-term population regulation of this kind was evolutionarily feasible, nonbreeding might seem to be a better mechanism than squabbles or interventions among the valuable adult stock; but nonbreeding may be physiologically difficult to achieve in mature individuals.

Breeding in long-lived seabirds, where adults are relatively non-expendable, raises questions concerning the stressful effects of the reproductive cycle, the possible occurrence of "rest-years," and the period of deferred maturity. For sulids the most demanding phase of the breeding cycle, judged by loss of weight, is not the feeding of the young but the pre-laying and, possibly, the incubation periods. For the male, the former involves strenuous display and long periods

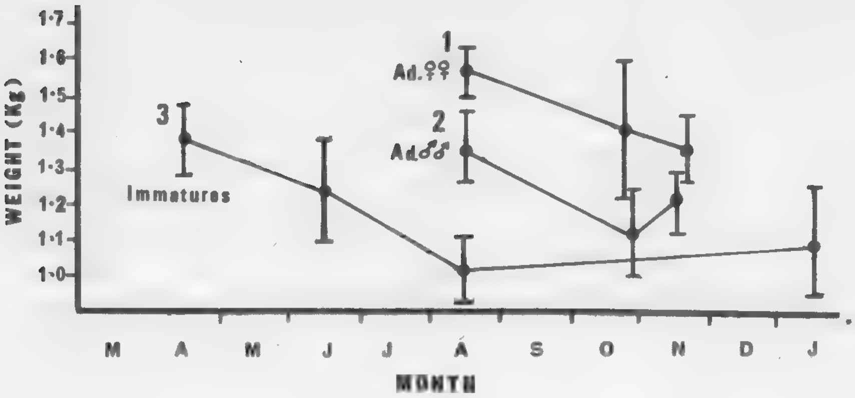


Figure 9. Seasonal changes in the weights of the Greater Frigatebird (*Fregata minor*) on Aldabra Atoll, Indian Ocean. The groups considered are adult females (1), adult males (2), and immatures (3). Data are taken from Diamond (1971).

of attendance at the colony; and for the female, the production of the egg. Diamond (1971) recorded the heaviest weights for frigatebirds when they returned to the colony to breed (Figures 8 and 9; see also Table 6). Both *ariel* and *minor* males lose weight until about October and then, when feeding young, gain again. The display and incubation periods are definitely stressful. Males of *minor* may occupy the same display perch for at least three consecutive days and the female's pre-laying unbroken stretch of attendance at the nest may be 10 days. During incubation, *minor* adults on the Galapagos lost up to 20 percent of their weight in a single incubation stint. This did not apply to the colony of *minor* on Aldabra.

There is little information on the two other points raised above. Rest-years may not occur; the high rate of failure may make them unnecessary; but in any case it is extremely difficult to prove for any seabird that a year in which it fails to breed is a "rest" year. There may always be some other reason, such as loss of mate.

The age of first breeding is at least five to seven years, probably nearer the latter. Juvenal plumage is retained until well into the third year; immature stages last another two years, perhaps more; and there may be a pre-breeding period in adult plumage.

Dispersal

The newly independent juveniles of *minor* disappear from the immediate vicinity of the breeding area on Tower and Aldabra, and this probably occurs in other frigatebirds, as well. At least some of them are highly nomadic. An Aldabran *ariel* was recovered in Bombay 4,400 km to the northeast less than a year after becoming independent (Diamond, 1975) and Sibley and Clapp (1967) reported 79 recoveries at varying distances from the Central Pacific breeding islands. Most had fledged three to ten months before. Immature birds, probably at least 22 to 23 months old, but still in juvenal plumage, returned to Aldabra in some numbers. On Tower, some immature males attended the fringes of displaying nuclei.

Immature and adult frigatebirds are frequently recorded far from land (up to 1,500 km), and the oft-repeated assertion that they remain within sight of their breeding colony is far from universally, if ever, true. They have never been recorded roosting on water, but gather in dense groups on bushes, trees, rocks, or the edges of cliffs, often in thousands, and on islands where they do not breed.

Behavior

Vocalizations and Mechanical Sounds

At the colony, frigatebirds produce a confusing variety of gakkering, squealing, warbling, chuckling, reeling, twanging, and clapping sounds. They are most usefully categorized by context. In *minor* a male utters a high pitched warble or whinny during his sexual display; the female has a more nasal counterpart. Its equivalent in *andrewsi* is a slower and deeper *ow-ee, ow-ee* which, played back on a tape at faster that normal speed, is virtually indistinguishable from *minor's* warble. *Magnificens* and *ariel* are said to lack this vocalization. Instead of the warble, *ariel* males give a rapid whistle when displaying (like the incoming or arrival call described below), while *magnificens* "reels" and "drums." Only noisy bill clapping is mentioned for *aquila* as an accompaniment to display but no doubt it also vocalizes. This adds up to a somewhat puzzling comparative picture, for it is difficult to understand why two of five frigatebirds should have evolved the "warble" or three lost it, when the accompanying homologous display among the five species is similar in almost every detail. Aggressive male *minor,* for example, when defending against intruders or descending to displace them, have a fairly high pitched twanging note; the female's again is horser. I phoneticized a somewhat similar incoming call in both male and female as *clew, clew, clew*. . . . It occurred in aggression-eliciting contexts. Diamond (1975) rendered the incoming call as *teeeeu-teeuu-teu* in the male and *wiiiick-wiick-wick* in the female. He rendered the equivalent call in *ariel* as a series of short whistles in the male and a hoarse *chuck-chuck-chuck* in the female; and in both sexes of *magnificens,* as a rapid rattle descending in pitch and increasing in speed.

In the male *minor* and *ariel* a fine reeling call, like a fisherman's reel unwinding, accompanies display and is delivered with parted mandibles, but may be mechanical. If the lower mandible tip touches the inflated sac, resonance imparts a different tone to the sound. Bill-clattering or clapping is mechanical and occurs in sexual and aggressive contexts. *Magnificens* "reels" but Diamond (1973) also describes drumming, a resonant sound heard only from birds with inflated

TABLE 6
Weights of *Fregata minor* on Tower Island, Galapagos, 1964, Showing Seasonal Variation in Adult Weight and the Decline in Weight of Free-flying but Partially Dependent Young

Status	*Mean weight and sample size*	*Range*
Adult male:		
Before egg-laying	1,217 (12)	950-1,450
With egg or chick	1,375 (2)	1,300-1,450
Adult female:		
Before egg-laying	1,621 (7)	1,400-1,850
With egg or chick	1,640 (6)	1,440-1,950
Free-flying but partly dependent young in:		
April	1,083 (9)	950-1,350
June	988 (13)	650-1,350
July	983 (12)	640-1,290
Freshly dead juveniles in July	590 (3)	550-640

pouches, and purring, which may simply be an attempt at drumming with a partly inflated pouch. Since drumming alternates with reeling, it may be the functional equivalent of the missing "warble." *Andrewsi* does not reel, but clatters mandibles noisily. It has a deep, hoarse, disyllabic incoming call not markedly different in the sexes. Gibson-Hill (1947) says *andrewsi* has a raven-like croak during display and ultimately deflates its pouch with a long, banshee-like wail. " . . . the noise from a group rises and falls and changes from predominantly clattering to mainly wailing and back again. The general effect is perhaps nearest to the combined noises of fighting donkeys and chattering monkeys mingled with the enthusiastic cries of the supporters of an American football team."

The young of all species possess an unpleasant screeching, squealing noise that is grating and tremulous. It is used as a food-begging call and at high intensity by chicks defending themselves.

Breeding Strategy

Many seabirds are typically faithful to the same site and mate each year, but this fidelity is geared to temperate and/or climatically seasonal environments and their correlated annual breeding cycles. The conditions in relatively aseasonal zones presumably make it less advantageous to time events and laying usually has a wide spread with no annually consistent peak. Under such circumstances, a bird can evolve one of several systems: (1) It can occupy a territory permanently, maintain its pair bond, and breed opportunistically at somewhat irregular intervals as does the Brown Booby on Ascension (Simmons, 1970) and the Blue-footed Booby (*Sula nebouxii*) in the Galapagos; (2) alternatively, it can disperse after a breeding attempt and return faithfully to the general breeding locality but propably will change its site and/or mate, as found in some populations of White Boobies, *Sula dactylatra* (Kepler, 1969), and probably some tropical terns and albatrosses; (3) finally, it can dispense with all long term ties to a specific territory and mate and return merely to the general breeding area or even to a different island. The strategy adopted will relate to the overall selection pressures acting on the species.

Because of their long breeding cycle, frigatebirds have evolved variants of the third procedure, with far-reaching implications. When parents guard the nestling, they necessarily see each other when one bird relieves the other at the nest. Once they stop guarding the nestling, adult frigatebirds may hardly meet again for the remainder of the long breeding cycle. Each parent now spends almost all of its time away from the colony. After completing the cycle, they enter the resting phase, again largely away from the breeding area. During the late stages of feeding their flying young, another portion of the population begins to breed in the same area. Subsequent re-pairing on the original site is thus highly impracticable. Take for example, a pair (X) of *minor* laying on Tower Island in February. If successful, they will be feeding their free-flying offspring in February of the following year, by which time breeding birds will be courting and laying, probably near, or actually on, pair X's site. The male's behavior precludes his chances of linking up with his former mate two years after he began nesting; for he joins a nucleus of nuptially adorned males and displays communally and unselectively to female *minors* that fly overhead. Only the female exercises a choice of mates. Unless she is around at precisely the right time, her former mate will already be paired. Nevertheless, the possibility that she does coincide her arrival with that of her mate's in the general area, and seeks him out, cannot yet be totally dismissed.

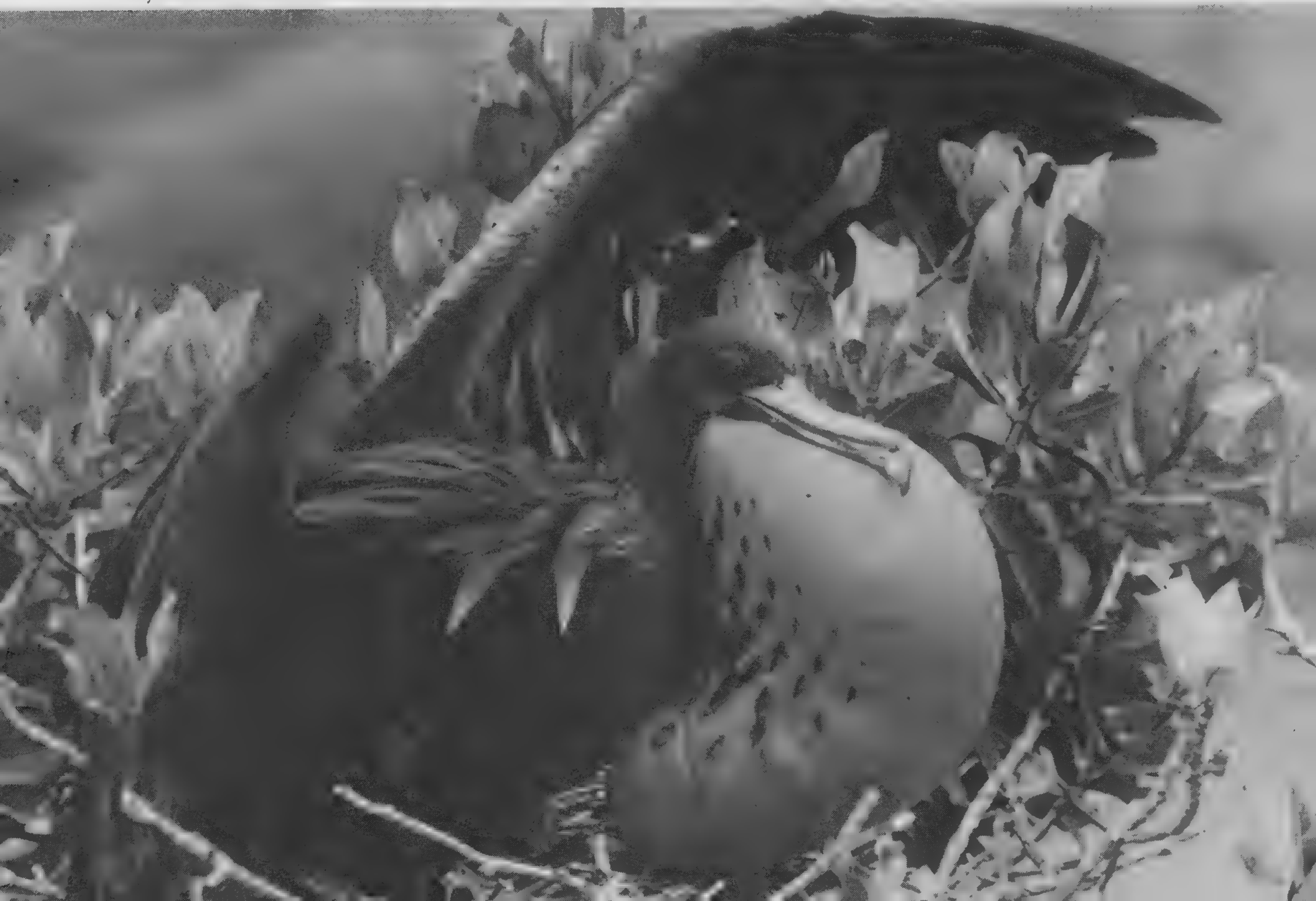
Displays

All five frigatebirds use basically the same displays. Species differ merely in the frequency and amplitude of the constituent motor patterns and associated vocalizations. However, subtle ethological isolating mechanisms probably are not necessary to prevent hybridization between sympatric species. Size, external features, vocalizations, and nesting habitat can readily do so.

The displays take place within the context of the following events and circumstances: adult males in nuptial plumage and with hugely distensible crimson gular sacs appear in the breeding area, which is occupied largely by free-flying juveniles. One or two males take up stations, usually near an old nest, and begin to display to over-flying females. This apparently stimulates other males to join in and a display-group grows to number as many as 30 or more individuals. Some males successfully form pairs and build on their display site. The others leave the group and display elsewhere. Once a male starts to build, he displays aggressively to intruding males. Males displaying in groups are, however, not hostile to each other within or between groups and are commonly in bodily contact. Thus, the space around a displaying male is, at this stage, not a defended territory, as is the equivalent space around a densely nesting sulid. Indeed, it is highly transient. On the other hand, display, though communal, is not cooperative. When a single over-flying female triggered violent display from 30 males, as I observed on Tower Island in the Galapagos, they responded independently.

The sexually motivated advertising display of males in *minor* is a Gular Presentation (Figures 10 and 11) and has three main elements: (1) an upward presentation of the inflated crimson pouch with the head thrown back and turned from side to side; (2) trembling of the spread wings, the silvery undersurfaces facing upwards; and (3) accompanying vocalization, described as warbling or whinnying, a rapid falsetto *whoo-whoo-whoo*. The wing-trembling is

Figure 10. The principal advertising displays involve the inflation of the bright red gular sac by males. Gular Presentation here is by a male Greater Frigatebird on Tower Island, Galapagos.



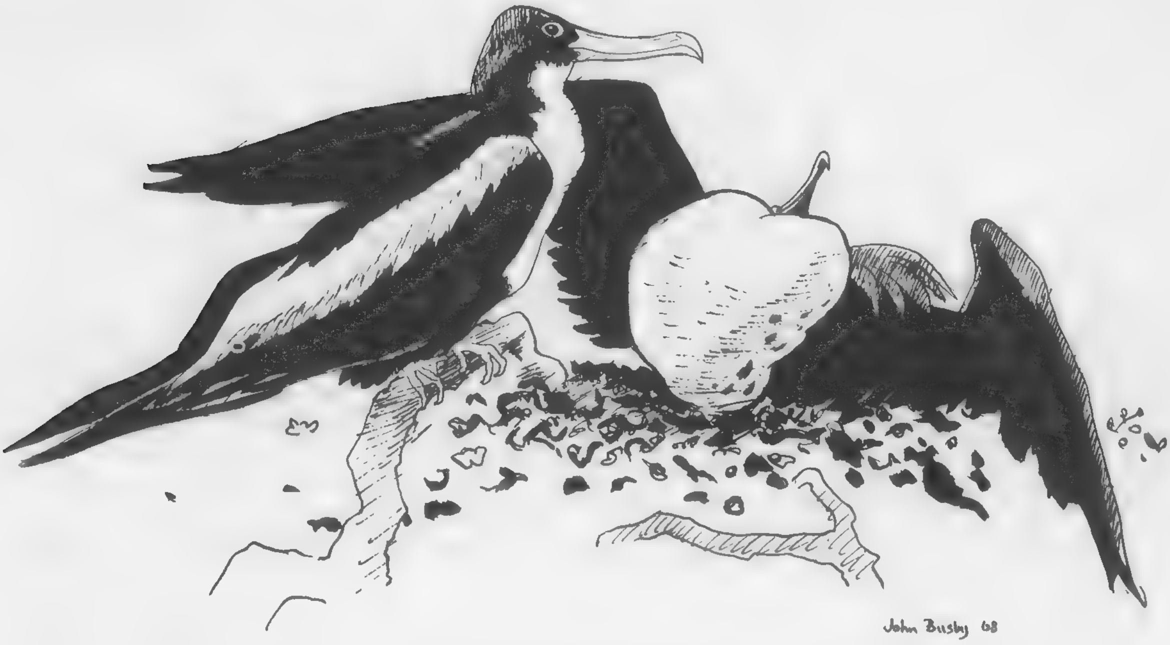


Figure 11. Gular presentation by a male Greater Frigatebird to a female that has just landed. Drawing by John Busby.

striking, for the males swivel on their perches as they orient their display directly toward the female, giving the effect of two enormous, beseeching black arms with the crimson sac couched between. If the female descends, the male's head-waving becomes more exaggerated and disjointed. A fine-drawn reeling sound and mandible-clapping, sometimes interspersed with a peculiar quavering sound, accompanies the display. Any one of three such conspicuous components would be dramatic; they produce an astounding performance when delivered by a group of birds. Males discriminate between females of different species and ignore juveniles, all, presumably, on the basis of their differently patterned ventral surfaces. (Figure 1).

The Gular Presentation functions mainly to attract a female to close quarters although, like the analagous advertising in sulids, it may also be performed after pair-formation. Occasionally, males actually thrust their display on the attention of disinterested females by landing on the nest and displaying. Rarely, females perform a version of the same display.

Frigates have no other display as highly ritualized as the Gular Presentation. However, the behavior of the pair, once in contact, is highly stereotyped and may be termed Mutual Head-waving (Figures 12 and 13). The movement is similar to that which the male uses when turning his head from side to side in Gular Presentation; the upward orientation of the bill typically persists. The birds make no attempt to maintain bill contact although, as they wave their heads, bills clash and heads may pass under, or occasionally over, the neck of the partner. The female's bill sometimes touches the male's gular sac, but one may doubt whether, as has been claimed she "caresses" it! Intermittently, and probably most often after the female has made contact with the male's sac, he grips her bill. The wings of the male usually are still outstretched from Gular Presentation but the female may keep her's folded. Outbursts of warbling, with a hoarser equivalent from the female, or a chuckling or quavering note and reeling and mandible-clapping all accompany Mutual Head-waving. There is some desultory nibbling of each other's plumage, which, as in sulids, may be a low-intensity expression of aggression. Functionally it is certainly not concerned with feather care. Occasionally, only the head makes contact with the partner's plumage and it may be that this "pleasurable" tactile stimulus has turned head wagging into a pair-bonding activity.

This simple ceremony is all that paired frigatebirds perform, and they keep it up for hours, including all through the night, with new outbursts occurring after quiet periods. They sometimes use it with a chuckling sound when changing over at the nest. Occasionally, however, they omit any greeting ceremony. Their pair-bonding behavior is thus "primitive," loosely ritualized, and limited in the scope of its behavioral dialogue in the sense that the partners perform only one, poorly differentiated mutual interaction compared with a wide range of pair-bonding interactions of the sulids and albatrosses. This is understandable in view of the pair bond's impermanence.

Often, a female investigates a group of displaying males, lands by one, but quickly leaves again. If she stays, the next few hours or even day or two are spent in almost constant company with the male, with frequent outbursts of head-waving and calling. Diamond (1975) describes a brief (few seconds) ritualized "gooseneck" action performed by female *ariel* when they approach displaying males. The female stretches her neck forward and sharply down, vibrates the wings rapidly and wags the tail from side to side. The wings are held flat and straight or even bent slightly forward. Nothing like this has been described for any other frigatebird.

There are no obvious preliminaries to copulation, during which the male spreads his wings, pecks the female's head and nape, and tramples. Brief head-waving often follows. Then the male begins to bring nest materials and the female, or the pair jointly, build it into the nest. The male brings nest material during incubation after the change-over at the nest. In all frigatebirds, the males bring more nest material than the females, although the difference may be much less marked than in *minor* (Galapagos), where I only once saw a female gather nest material.

Aggression, Site-selection, and Pair-formation

The display perch is not a conventional territory and in many cases is abandoned without having led to pair-formation and nest-building. However, once pair-formation has occurred and nest-building begun, both males and females react aggressively to intruders by lunging, snapping, calling, and displaying. In the display, a modification of the Gular Presentation, the wings are spread and waved but not vibrated as in the Gular Presentation; and the note is not the warble, but the aggressive "twanging" or *clew clew* often followed by the reeling noise.

Actual fighting between males, although not uncommon, is fairly mild and usually lasts less than two minutes. I have many records of up to four males involved in concerted or successive attacks on a nest-owning male followed by fighting among themselves. It is difficult to crystallize the typical pattern of events, but the momentary disclosure of the nest itself undoubtedly acts as a common trigger to the fighting. Over-flying males react swiftly when a nesting bird makes even an intention movement of leaving. Literally within two seconds, I have seen intruders descend and actually attack the nesting bird by pecking and grappling. Events become complicated and at the end there may be one male—

not necessarily the owner—on the nest and three former combatants gracing the bushes absolutely motionless with great wings asprawl.

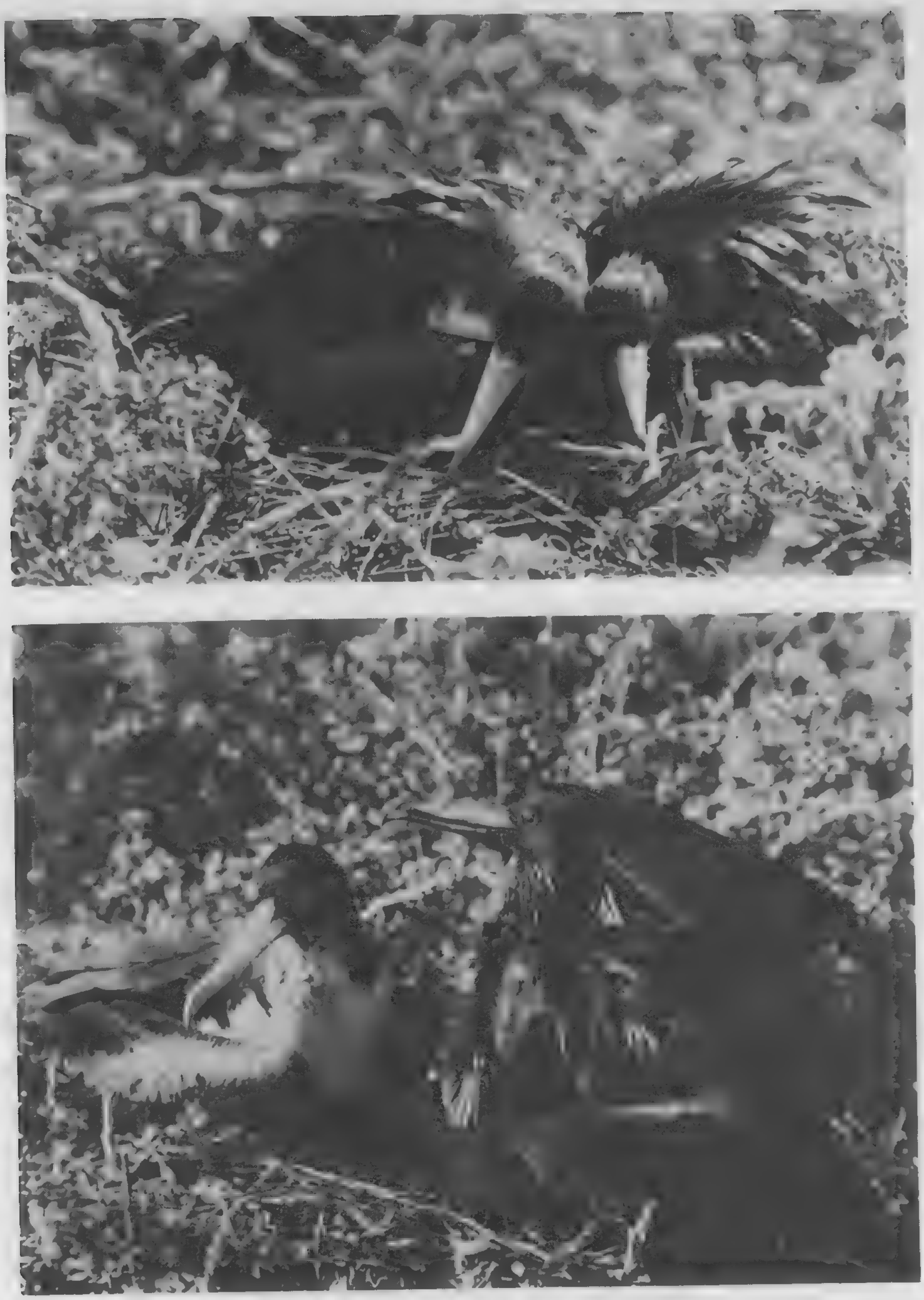
This attempted usurpation is not simply pilfering of nest material, although that, too, is common, but is an attempt to take over the nest and site. Frigatebirds have no display that serves to proclaim site ownership before a threat of attack. This may be an inevitable consequence of initially transient display sites, but one result may be that potential intruders do not receive any clear signal communicating the status of the male on the nest. Males obtain a partner on the display perch, which is not formally and consistently defended; nor do mates then abruptly begin to defend the site by ritualized display. Indeed, although males often react aggressively to intruders, their lack of territorial defense on other occasions is nothing short of astonishing. For example, a male *minor* returned to his unguarded nestling to find an intruder attacking it. Instead of driving the attacker away, the owner simply perched nearby, apparently unconcerned, but immediately fed the nestling after we displaced the intruder.

Aggression between a mated pair also shows unusual features. Little overt aggression occurs between the prospective partners, although males intruding on paired females may be violently pecked, and intruding males that have displaced an owner may, in turn, be attacked and displaced by the resident female. No ritualized appeasement or repetitive departures and returns occur in frigatebirds as they do in all sulids. The conflict between aggression and fear in birds, often a source of ritualized display between members of the pair, seems unobtrusive in frigatebirds. One is tempted to suggest that the down-grading in importance of the site and pair-bond is reflected in the poverty of the associated behavior. Presumably it would be difficult to evolve the habit of communal, non-territorial display along with subsequent and sudden development of territorial defense on the same site. Linked with this, there would be no advantage in evolving a system of complex and repetitive behavior whose function would be to condition the female to strong attachment and defense of the territory. This system, while present in the boobies, is absent in the frigatebirds. The marked sexual dimorphism in frigatebirds seems to be consistent with this interpretation, for where sexes are similar, both parents often vigorously defend a territory; the gannet is an extreme example.

Egg loss on Tower Island usually stemmed from interference by males, and within minutes a male with an inflated sac often sat on the empty nest with the egg, or sometimes a nestling, lying beneath. Usually I did not witness the actual loss of the egg but returned shortly after a previous check to find a displaying male or pair. In such cases, the rightful male had been displaced. Occasionally, egg-loss followed a change-over at the nest and the male started displaying again only after sitting on the site for several days with a shrivelled sac. In these cases, the female often replaced the egg and the pair started incubating again. Twice, I marked a female and removed the egg and in both cases a new male took over; the original female did not return.

The pattern of sexual display described for *minor* applies closely to all other frigatebirds. Details are published only for *magnificens* (Diamond, 1973), but Stonehouse (1963) says enough for *aquila* to establish the similarity, as does Diamond (1971) for *ariel*. My own observations for *andrewsi* confirm that it also displays like *minor*. Similarly, the prevalence of nesting interference by displaying males is also obvious in all species except possibly *andrewsi*.

As mentioned, Diamond (1975) states that *magnificens* and *ariel* lack the vocal "warble," but *andrewsi* possesses an equivalent. On Barbuda, *magnificens* displayed



Figures 12 and 13. Mutual Head-waving display, a highly stereotyped pair-bonding interaction following successful gular display by the male.

in groups of four to eight males and displaying males apparently resisted attempts by others to join the group. In this sense they defended their position, but did not show a site-ownership display. Probably displaying males of *minor* will lunge at others attempting to land too near, but will not defend the site, as such, if not actually displaying on it; nor will males object to actual physical contact with other displaying males. Like *minor*, the male *magnificens* uses a display against intruders similar to the sexual one, although the display lacks the stereotyped wing-trembling, thrown-back head, and raised scapulars.

Pair-bonding in all species incorporates Mutual Head-waving with occasional and brief unilateral allo-preening (female to male). Only in the Mutual Head-waving can frigatebirds of both sexes be said to have a similar display (Van Tets, 1965).

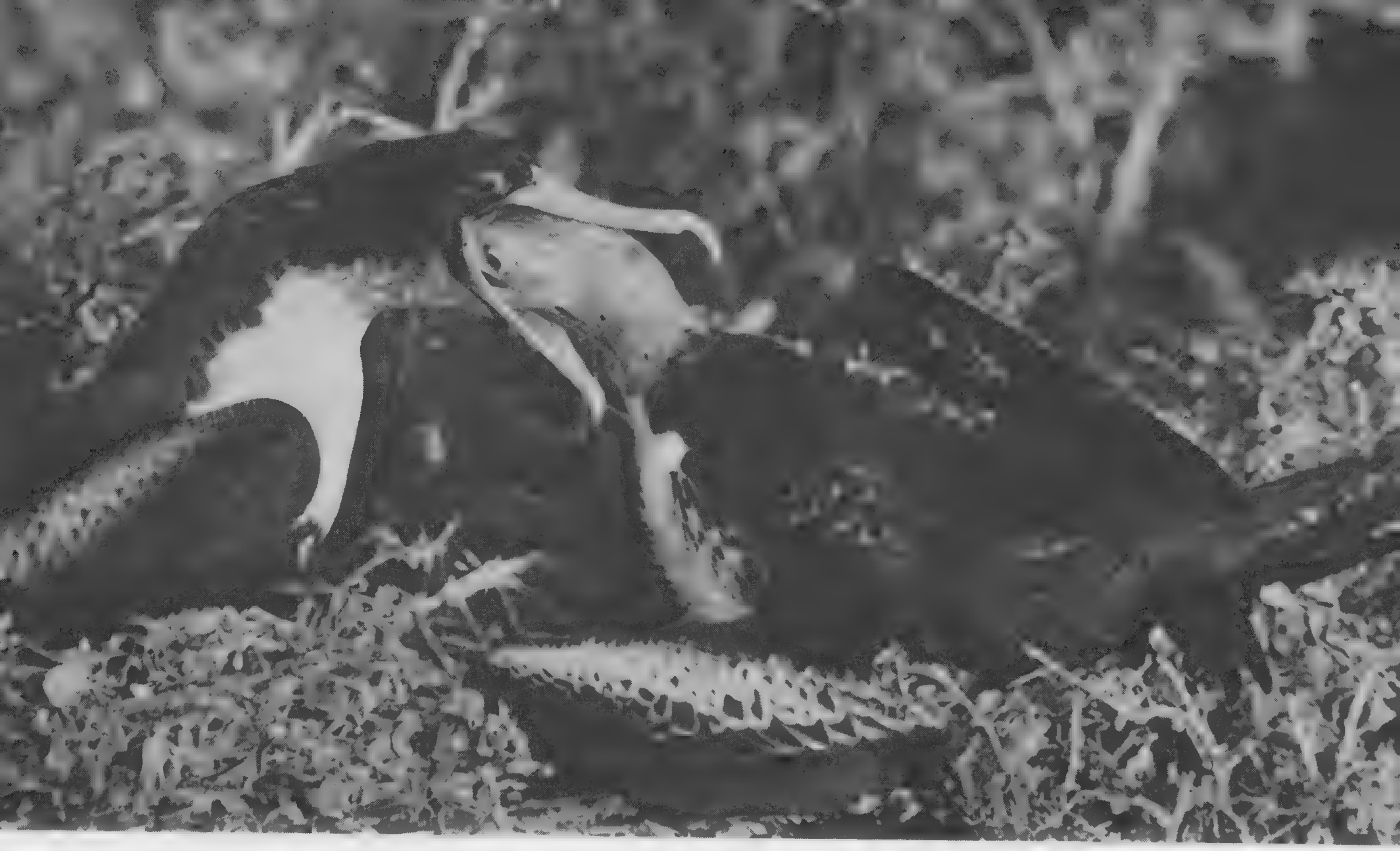


Figure 14. A free-flying juvenile reaches into the female's mouth for food, often a bolus of flying fish.

Incubation

The sexes share incubation equally, the duration of attentive periods varying with species and locality. On Aldabra and the two Christmas Islands (Indian and Pacific Oceans), individual birds (*minor*) incubated for about four days at a stretch, but in the Galapagos, bouts of incubation ranged from 3 to 18 days, averaging 9.5 days in males, 11.5 days in females. *Ariel* on Aldabra sat for two to six days. *Andrewsi's* sitting periods averaged only two to three days. It seems that in all frigatebirds, attentive periods are long or very long, and early accounts of each sex sitting for half a day at a time are mistaken. It is probably valid to assume that while one partner incubates, the other forages, and that incubation stints are thus useful ecological indicators. However, a relieved bird does not always go straight to sea, but may first go to a roosting area to preen.

I interpret the long attentive periods during incubation to mean that, in view of their impoverished feeding habitat and specialized mode of feeding, it is more economical for frigatebirds to spend several days foraging until they have found enough food to replenish their reserves, than to make a number of hurried and perhaps fruitless or only partially successful trips lasting a few hours each. In addition, the reduced frequency of change-overs resulting from long attentive periods, reduces the chances of dislodging the egg from the nest platform. The tendency towards simplicity in behavior between the pair is evident, too, in the frequent absence of a greeting ceremony or, indeed, any ritualized interaction during nest-relief.

Care of Nestling

The nestling is fed by incomplete regurgitation; that is, the parents regurgitate food from the esophagus and stomach into the mouth, from which the young removes it with its bill (Figure 14). Gibson-Hill (1947) reports that adults dribble fluid into the open bill of a small nestling rather than opening their mouths for the insertion of the nestling's bill. It is brooded for up to about five weeks. After that, although still virtually defenseless against intruding frigatebirds or a determined predator, the parents leave the nestling unguarded. Parents first left their nestlings unguarded on the Galapagos (*minor*) when the latter averaged 31 days of age. Some *aquila* left their young at ages of 10 to 15 days, when nestlings suffered their heaviest mortality from harassment by other frigatebirds (Stonehouse, 1963). One wonders how much mortality in this case was due to human disturbance, since at that age young frigatebirds are incapable of thermo-regulation. On Tower Island, adult males killed 9 of 37 (24.3 percent) nestlings during the first spell in which they were unguarded by the parents.

The frequency with which parents feed their nestling varies with locality. On Christmas Island (Indian Ocean), *andrewsi* received food each day or once every two days. In the Galapagos, *minor* nestlings sometimes went for several days without food and were fed on the average about once every three days. *Minor* and *ariel* on Aldabra fed their young once every 2.3 and 2.4 days, respectively. Food may be delivered at any time of day or during the night; but Diamond (1971) found that *minor* chicks were fed mainly between 09:00 and 12:00 hours and *ariel* chicks in the afternoon, although sex differences in the timing of feedings complicated this general pattern. He recorded that, due to the tendency to feed less in the afternoon, the male *minor* fed nestlings less frequently than did the female. This trend was extended in *magnificens* on Barbuda, in which the males virtually abandoned the colony in June, five months after the end of the peak laying period in January, leaving the female to cope with the nestling. Large young of all frigatebirds beg in a restrained manner, relative to comparable behavior in boobies, with spread wings, a hunched posture, up-and-down bobbing, and harsh squealing. Parents eventually recognize their own young and discriminate against interlopers.

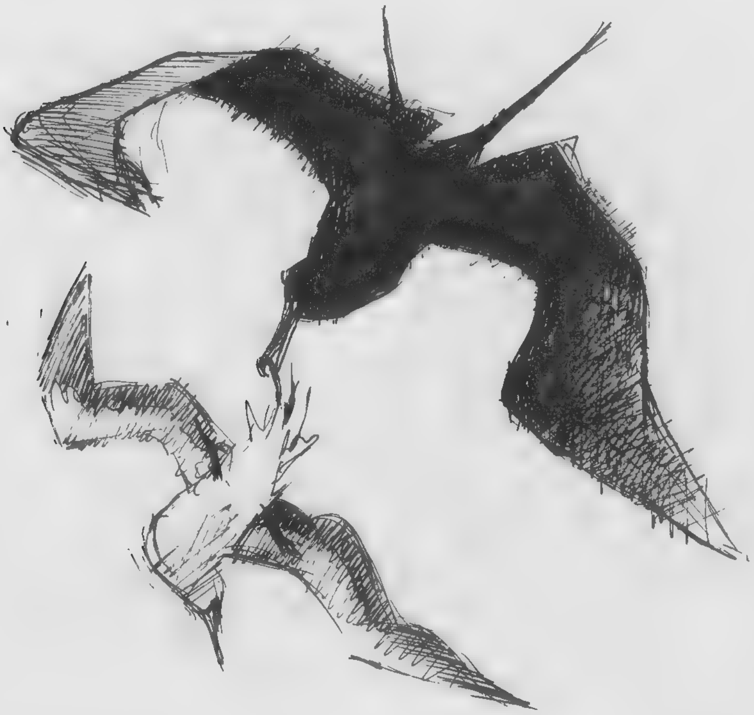


Figure 15. A Greater Frigatebird "tipping" a booby to force it to regurgitate. Drawing by John Busby.

Painting by John Busby of young Lesser Frigatebirds *(Fregata ariel)* on Aldabra, Indian Ocean.

The free-flying dependent juveniles of both *minor* and *ariel* spend at least one-quarter to one-half of each day at the colony. Presumably, they supplement parental feedings by their own efforts but there are no quantitative observations on this. Dependent *minor* juveniles on Tower Island weighed an average 1,083 grams (850 to 1,350) in April and 983 grams (650 to 1,350) in early July. Several birds had starved by July, weighing an average 590 grams. It seems clear that, at least in the Galapagos, even after prolonged parental "subsidy," the young have difficulty attaining self-sufficiency.

Feeding Behavior

The adult frigatebird's acrobatic piracy (Figure 15) is so arresting that early observers wrote as though it were their sole method of feeding. In fact, a mere fraction of the food supply in any frigatebird population stems from this source, although some individuals may subsist mostly by piracy. The main considerations of feeding frigatebirds concern (1) the importance of piracy along with the behavior involved and cues that trigger it, and (2) the major methods of feeding and how they differ between species.

Conflicting reports exist about the nature, extent, and success of piracy. Undoubtedly, the principal victims are boobies, particularly Red-footed Boobies, whose distribution is closely matched by *minor*. However, almost any bird (gulls, terns, shearwaters, tropicbirds) may be chased by frigatebirds; and frigatebirds chase each other. Adults of both sexes chase, but unequally. In the Galapagos, males (*minor*) chased much more often than females; on Aldabra and Christmas Island (Pacific) females (*minor*) chased more than males (54:2); and on Aldabra, females of *minor* and *ariel* chased more often than males. In the Caribbean, female *magnificens* chased much more than males (Verner *in* Palmer, 1962). The percentage of successful piracies also seems to vary with locality. Twelve percent of the attempted piracies by *minor* on Red-footed Boobies were successful in the Galapagos, 18 percent on Aldabra, and 63 percent on Christmas Island (Pacific). However, all these figures refer to chases near the colony. At sea

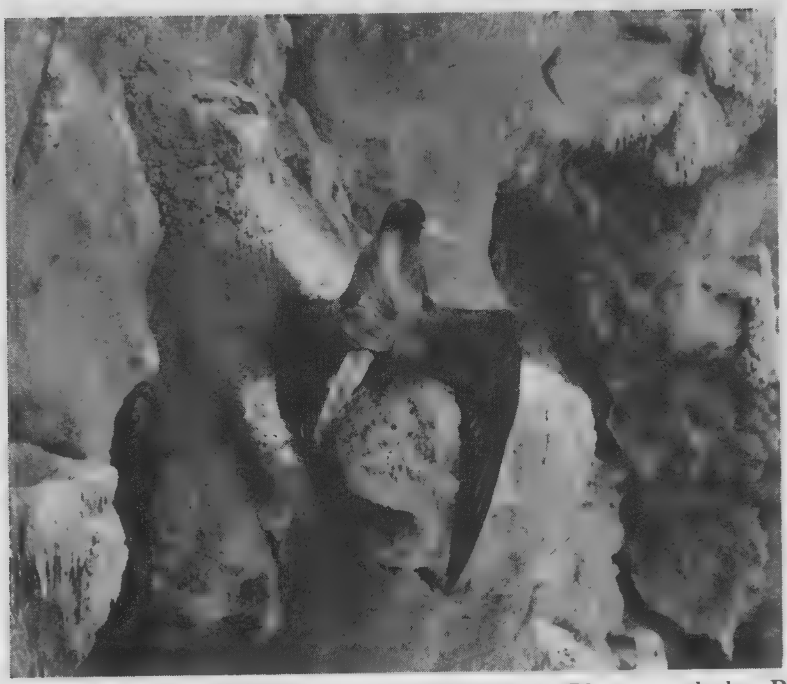


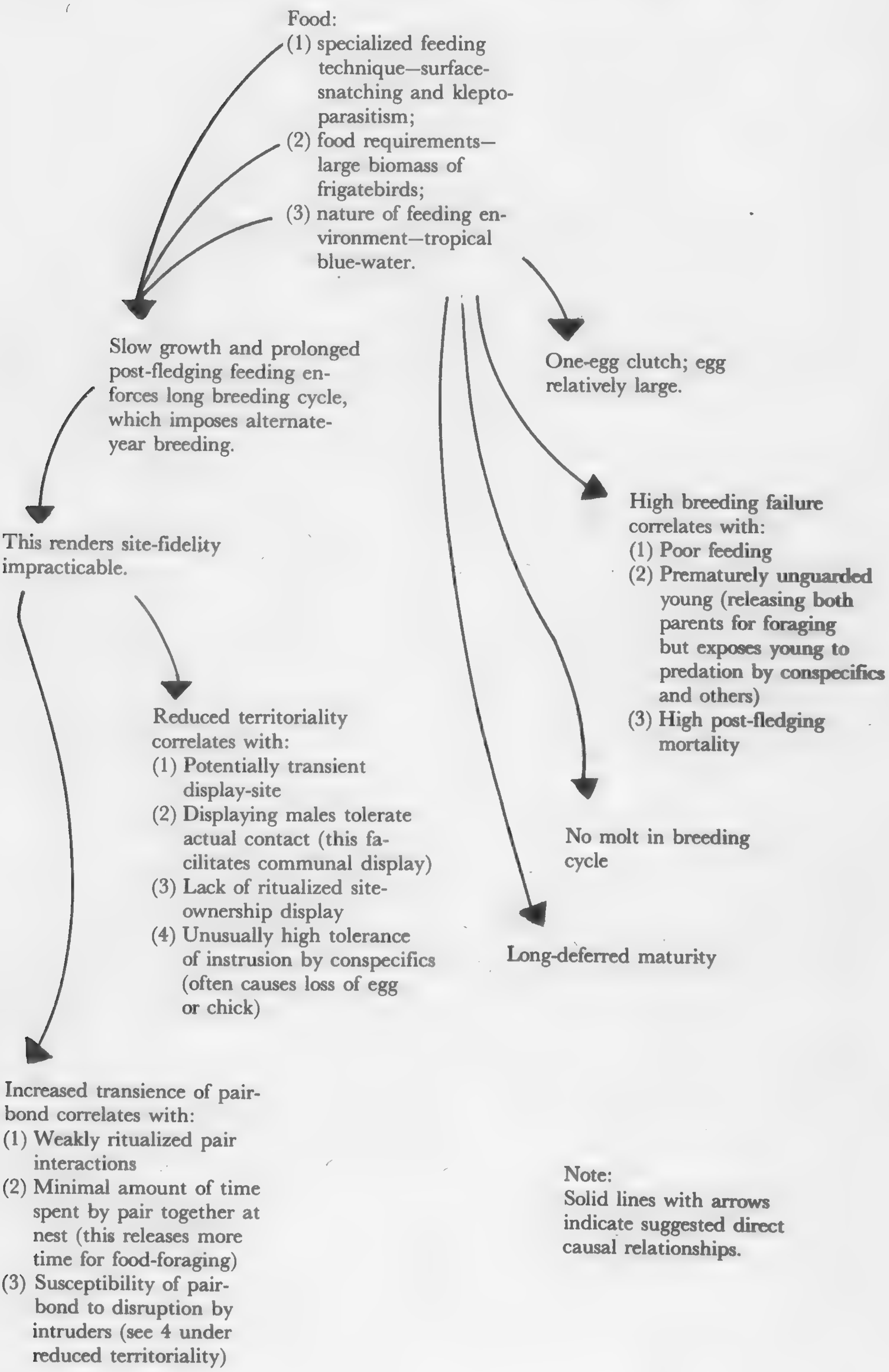
Figure 16. An Ascension Frigatebird (*Fregata aquila*) sunning. Photograph by Phillip Ashmole.

the picture may be different. Most chases occur when boobies are returning in the afternoon and evening with full crops. Frigatebirds do not chase indiscriminately. Often they quickly abandon a pursuit, presumably on some cue that could be the nature of the booby's vocalization; a full crop may impart a distinctive quality to the alarm call. Immature frigatebirds play with objects in the air, taking them from each other or dropping and retrieving them. This practice must polish their motor coordination. They attempt the simpler forms of piracy while still immature, but dependent young are not known to do so.

Frigatebirds (particularly *magnificens*) take the eggs and young of their own and other species, snatch carrion and offal from the water (recorded for *minor, magnificens, aquila,* and *andrewsi*), and fly down and kill newly fledged young of small seabirds such as shearwaters. An unusual food item recorded was grasshoppers from the stomach of *andrewsi*, which are very common on Christmas Island (Indian Ocean). The frigatebirds probably picked them up from the vegetation near their nests. Apparently the strength of *minor's* tendency to prey on temporarily exposed eggs and young of its own species varies with area. On Aldabra it is rare, although adults pilfer nest material. They take young turtles in the shallows or on the way to the water. Frigatebirds are reluctant to snatch food from the ground, but do so on occasion. However, all these are unimportant opportunistic events. The frigatebirds' main food is flying fish and squid, which they catch at sea by surface-dipping. The only study of the composition of catches by frigatebirds is that of Diamond (1975) for *minor* and *ariel* on Aldabra. One would anticipate that the distinctly smaller *ariel* takes different prey from *minor* or at least a different size of prey. However, Diamond found that the difference was far less straightforward than that. No overall difference existed, but *ariel* took more squid than *minor* in the wet season, while in the dry season the two species took different proportions of the two main genera of flying fish (*Exocoetus* and *Cypselurus*). In the dry season, Diamond found no difference in the size of prey taken by *minor* and *ariel*; but in the wet season, the smaller items taken by *ariel* represented a higher proportion of squid which are smaller than fish. Thus, differences between the two sympatric frigatebirds existed, but there was considerable overlap.

The inter-relationships suggested in this article are shown in the following scheme:

SUGGESTED RELATIONSHIPS BETWEEN THE NATURE
OF FRIGATEBIRDS' FOOD AND THEIR BREEDING BIOLOGY



Food:
(1) specialized feeding technique—surface-snatching and klepto-parasitism;
(2) food requirements—large biomass of frigatebirds;
(3) nature of feeding environment—tropical blue-water.

Slow growth and prolonged post-fledging feeding enforces long breeding cycle, which imposes alternate-year breeding.

One-egg clutch; egg relatively large.

This renders site-fidelity impracticable.

High breeding failure correlates with:
(1) Poor feeding
(2) Prematurely unguarded young (releasing both parents for foraging but exposes young to predation by conspecifics and others)
(3) High post-fledging mortality

Reduced territoriality correlates with:
(1) Potentially transient display-site
(2) Displaying males tolerate actual contact (this facilitates communal display)
(3) Lack of ritualized site-ownership display
(4) Unusually high tolerance of instrusion by conspecifics (often causes loss of egg or chick)

No molt in breeding cycle

Long-deferred maturity

Increased transience of pair-bond correlates with:
(1) Weakly ritualized pair interactions
(2) Minimal amount of time spent by pair together at nest (this releases more time for food-foraging)
(3) Susceptibility of pair-bond to disruption by intruders (see 4 under reduced territoriality)

Note:
Solid lines with arrows indicate suggested direct causal relationships.

Body Maintenance

In the heat of the day, frigatebirds of both sexes and immature birds often adopt bizarre sunning postures (Figure 16) while sitting either on a branch or rock. The function of this behavior has never been explained. Their habit of turning the under-surfaces of their wings to the sky, however, tempts the suggestion that they are radiating heat.

Conclusions

Throughout this account, the influence of an unusual reproductive cycle on the frigatebird's behavior has been evident. I have portrayed biennial breeding as the inevitable concomitant of a specialized feeding niche functioning under the particular conditions of a mainly tropical oceanic environment. The biennial cycle has determined the nature of territorial and pair-bonding behavior (Nelson, 1967). These behaviors may be even more aberrant than they seem, considering our current, inadequate knowledge.

Since there is no precise site fidelity, one might suspect that frigatebirds may change not only the nest site itself but the general location of nesting. It is now clear that they do so. On Aldabra, for instance, although the main frigatebird localities are inhabited every year, large numbers of adult *minor* and *ariel* move from one locality to another over a distance of several miles. By analogy, it is possible that these two species may change islands within an island group. This would be a unique phenomenon within the Pelecaniformes, although paralleled by some terns. Even more unusual is Diamond's (1972) suggestion that on Barbuda *magnificens* has evolved sexual dimorphism in the breeding role. He found that males disappeared from the colony part way through the nestling period and suggests that the females complete the rearing process on their own while the males breed again. It could plausibly be the loose ties to territory and mate, both of which result from the frigatebird's feeding specializations.

Summary

Frigatebirds are highly specialized for an aerial life, but show no major adaptive radiation in morphology. Plumage differences between species include different patterns of white on the undersurfaces in females. Males show much less or no white. Juveniles can be almost impossible to distinguish in the field. Females of the Lesser Frigatebird (*Fregata ariel*) and the Greater Frigatebird (*F. minor*) show dimorphism in the color of bill and eye-ring in some parts of their range, and within a single population in *ariel*. At least in *F. minor*, size varies in different areas. Andrew's Frigatebird (*F. andrewsi*) and the Ascension Frigatebird (*F. aquila*) are each restricted to a single island. The Magnificent Frigatebird (*F. magnificens*) is the only species found in the Caribbean and *minor* and *ariel* are widespread in the pantropics and often sympatric.

The specialized feeding techniques in frigatebirds have a pervasive effect on their breeding biology, particularly by demanding a very long breeding cycle, which in turn greatly affects the relevant behavior.

Colony size varies from hundreds or less, to upwards of 5,000 pairs. Immatures and nonbreeders may number thousands at some colonies.

Male frigatebirds attract overflying females by a Presentation display of the

scarlet gular sac. Males display in groups and show markedly little aggression to each other. Display sites are vacated by unsuccessful males who then join display groups elsewhere. Once the initial contact has been made, the pair forms a bond by means of a loosely-differentiated Mutual Head-waving display. This is the only obvious and frequent pair interaction in the pre-laying period, except for copulation. After egg-laying, the pair hardly interacts at all, even when changing over at the nest. Unmated males interfere drastically in the affairs of mated pairs.

As a family, frigatebirds nest on the ground, in bushes, and in trees, including dead ones, building only flimsy, fairly flat, twiggy platforms. Nests are clumped, although the size of groups and the distance between them is highly variable. All species lay a single white egg, comprising between five and six percent of the female's weight. Replacement of a clutch that is lost takes on the average about 14 days.

Laying, in all species except *andrewsi*, is prolonged. However, in some localities it is loosely synchronized. And in all species, there is marked synchrony within sub-groups. Probably, frigatebirds breed for the first time when at least seven years old.

The sexes share incubation. In the Galapagos, *minor* stints averaged about ten days, and some lasted 18. Elsewhere, and in other species, they are shorter.

The naked, altricial young grow slowly, becoming down-covered and black-caped in about five weeks but not completely clear of down until about 26 weeks old in some cases. They fledge at about six months. The age at which the young are first left unattended varies with species but is usually four or five weeks. The rate of growth varies between species, and between regions of the range in *minor*. Post-fledging dependency of free-flying young on both parents is extremely prolonged—probably nowhere less than six months and often a year or more. This varies from species to species and probably with area. Even then, newly independent young may starve. Males of *magnificens* in the Caribbean apparently cease feeding their young part way through the latter's growth. Young frigatebirds disperse widely, several thousand kilometers, from the area in which they were born.

Probably no more than 15 to 25 percent of the eggs laid yield fledged young, and further mortality may follow before the young become independent. Much, or most, of the egg loss and mortality of small young results from interference by conspecifics. In some areas, such as the Galapagos, predation may be important. Annual adult mortality is probably not more than four percent, thus yielding an average life expectancy of 25.6 years. Apparently, none of the frigatebirds have an annual cycle. They probably breed once every two years but possibly once every 18 months in some areas. They molt between breeding cycles. However, since the failure rate of breeding attempts is so high, possibly more than three-quarters of the adult frigatebird population begin a breeding cycle each year.

Kleptoparasitism is practiced mainly by females; the success rate is not high and most frigatebirds get most, or all, of their food by snatching flying fish and squid from the surface.

The habit of preying on eggs and young of other frigatebirds apparently varies with species; possibly *magnificens* is most prone to do it. The one study (Diamond, 1975) which compared the diet in two sympatric frigatebirds (*minor* and *ariel* on Aldabra) showed a slight difference in prey preference.

Probably all frigatebirds sun themselves, turning the undersurfaces of spread wings to the sun. The function of this behavior is not known.

Acknowledgments

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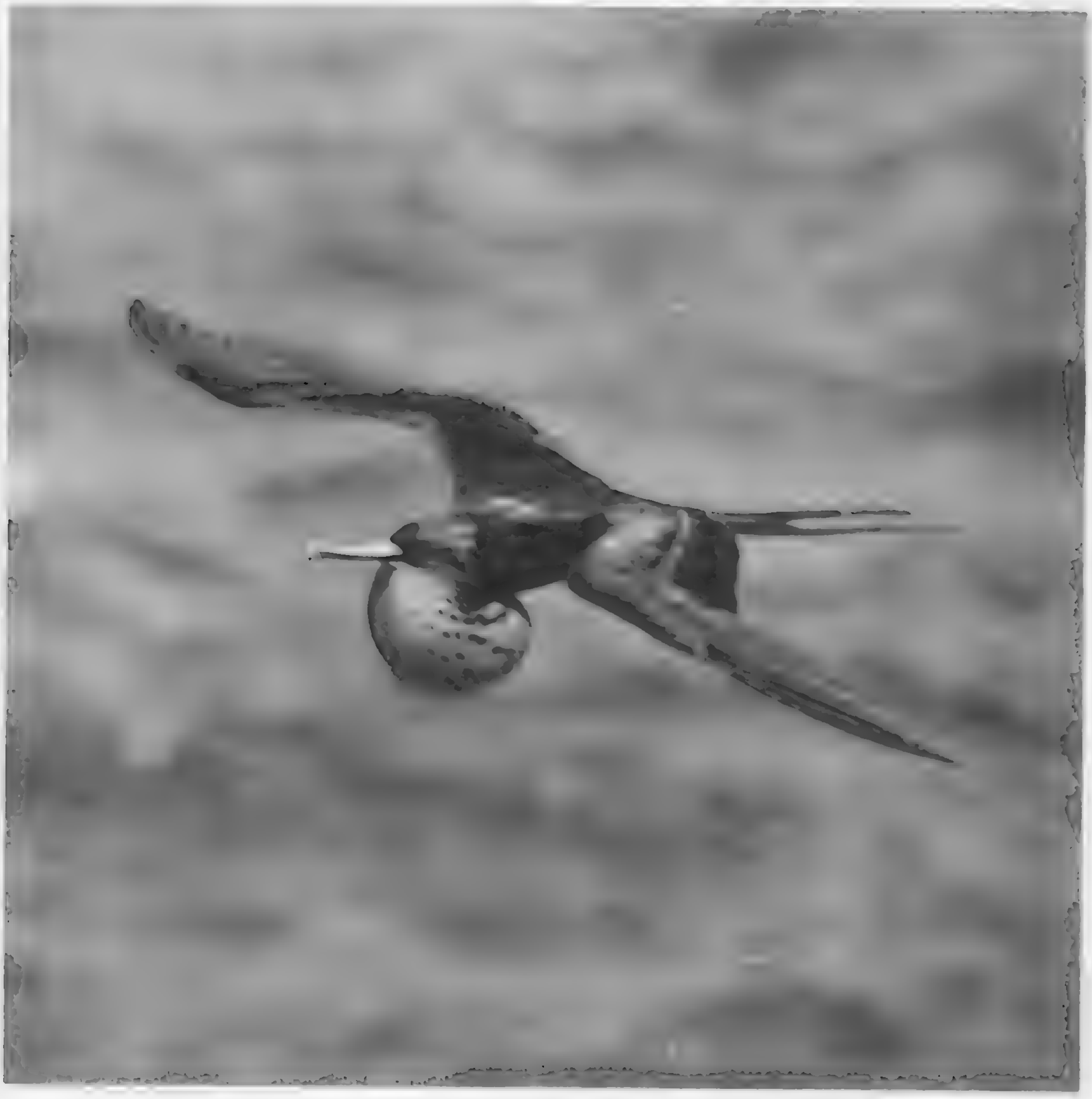

A male Greater Frigatebird *(Fregata minor)* with gular sac extended while flying at Christmas Island, Indian Ocean.

Frigatebirds in flight. Drawing by John Busby.

TERRITORIAL DEFENSE OF PEOPLE BY LAUGHING GULLS

PETER R. JUTRO

Gulls are opportunistic omnivores, feeding on a variety of food items, often scavenging, and habitually following boats and ships to pick up refuse thrown overboard.

While visiting County Beach on Siesta Key in Sarasota County, Florida, I observed immature Laughing Gulls, *Larus atricilla,* in their second year displaying a little-known form of social behavior. As people spread blankets on a public beach and settled down with bathing, picnicking, and sunbathing paraphernalia, I observed that single gulls landed within a distance of approximately three meters and initiated defense of a generally circular area around the people, the radius of the circle ranging from three to six meters for various birds.

Each Laughing Gull defended this area from invasion by other gulls. I observed nine instances of this behavior in mid-January, 1973, during an unseasonably cold period with few visitors on the beach, and only two instances during a normally warm January day in 1975.

To an intrusion into its territory, an immature Laughing Gull displayed an apparently consistent range of aggressive behavior generally identified with defense that included several threat displays and a long warning call. Depending upon the degree of response by the invader, the call was repeated, or the defending gull noisily charged the invader, running quickly with wings flapping, then stopped and called again. In all observed cases, invaders retreated after the threat displays and charges and no altercations were observed.

Defending Laughing Gulls challenged each territorial invasion. Within the first four minutes of each defense, the 11 defending birds that I observed repelled from 5 to 12 invaders. After an initial few minutes of defense, other gulls only rarely invaded established territories and were repelled by a threatening call.

A number of gulls congregated at the edge of the defended area. The observed territories appeared to grade over a one- to two-meter zone into "public space." Birds perceived to be outside the territory were ignored by the defender. If birds moved in through this transition zone, the defender's threat displays turned them back.

My observations indicated that a gull defended such a territory for approximately five to ten minutes if not rewarded. The gull then wandered off to feed elsewhere, and although gulls outside the abandoned territory

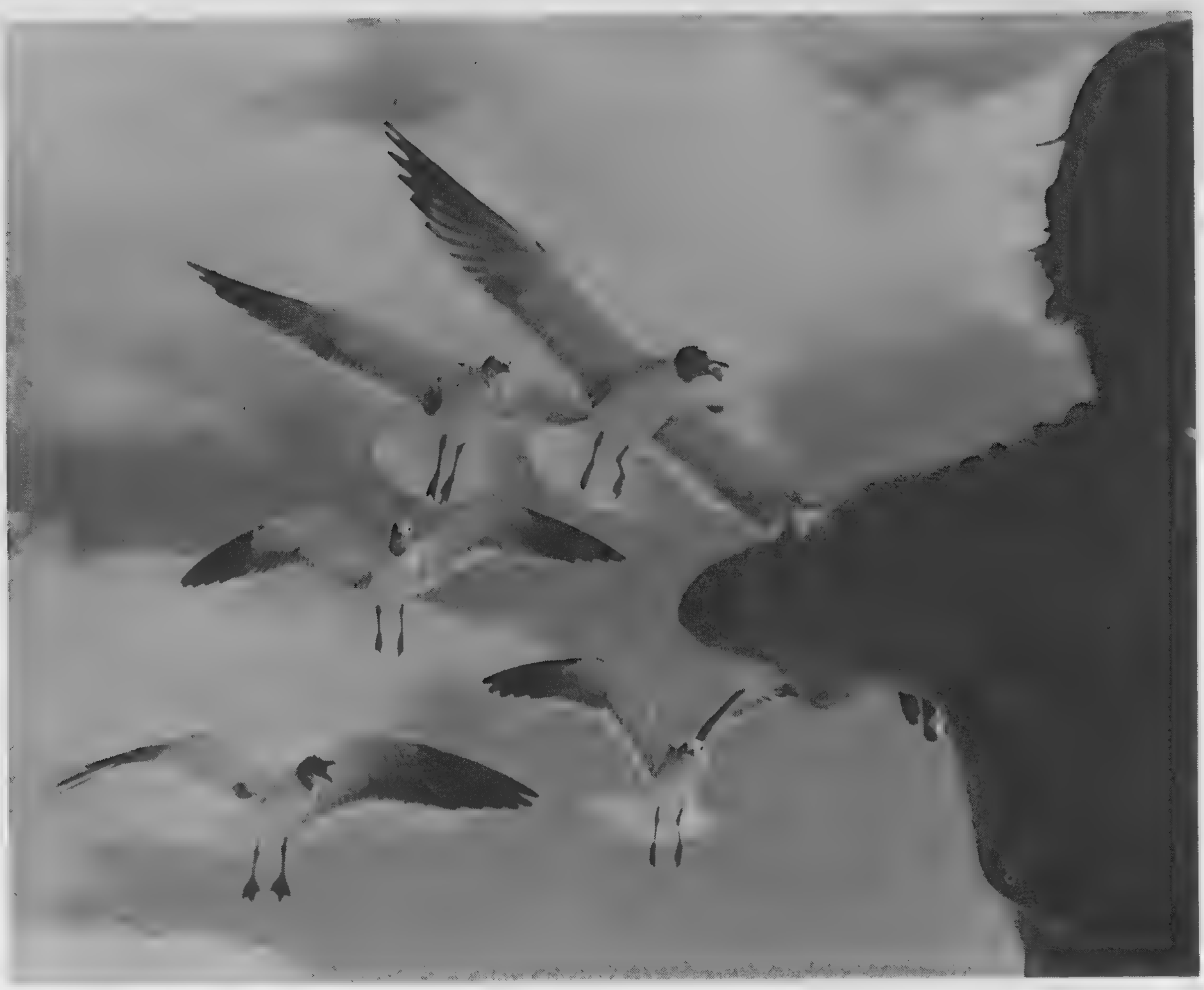

Figure 1. Airborne gulls hover near the extended arm of a person who tosses food scraps into the air. The closest gull is in the process of capturing a cube of bread that has just been tossed. The bread can be seen in its open bill.

sometimes entered it, none made attempts to exclude other gulls.

If, on the other hand, food was proferred following the establishment of a territory, the response was more complex. If a single scrap of food was offered, the bird took it, then looked around. If single scraps were thrown sequentially, this pattern was repeated with occasional warning calls if the feeding bird detected encroachment on the periphery of its temporary territory. If a handful of food scraps were thrown, however, behavioral conflicts arose between feeding and defending the territory. If the bird concentrated on feeding, peripheral birds moved in to take food. If a gull were to concentrate on defense, it probably would not be able to consume the food lying on the sand. The latter extreme was not observed, but the former, and intermediate behavior patterns, were.

Some territorial gulls immediately concentrated on eating and allowed other birds to feed simultaneously; other defenders quickly fed, called, took another scrap or two, called again; but in all observed cases, the gulls abandoned these perfunctory defensive actions within a few minutes, and territoriality "broke down." In only one instance did a bird attempt to re-establish exclusivity following a feeding, and he succeeded.

Although I repeatedly observed similar territorial activity, I usually did not record territoriality in what appeared to me to be potentially favorable situations. Not all human visitors, similarly encumbered and settling in sparsely occupied sections of the beach, were "adopted" by gulls. To some extent, this supports the hypothesis that this is newly learned behavior. It was never noted in previous visits. Although I noted this behavior pattern at widely separated areas on this stretch of public beach, I did not record it on nearby coastal areas that only rarely have human visitors.

Gulls are regularly fed by visitors to public beaches in this area. Persons often stand holding food with an arm extended upward. Gulls will take flight to take food from the hand and are regularly tossed food scraps by sunbathers and picnickers. I have seen as many as 100 gulls mob and compete for the limited amount of food offered by a person on the beach.

Whereas most gulls in such a setting eventually learn that people can be safe and consistent food providers, some of these gulls appear to have learned to identify potential feeders among people and to defend a territory around them in anticipation of feeding. Other birds have learned to respect this territorial defense, but simultaneously appear to recognize the advantage conferred by maintaining proximity. Considering the level of competition for limited food, there is an obvious energetic advantage in having exclusive access to at least the first bits of food offered, since in any given flock feeding situation, the majority of birds often receive no food at all.

The description of learned anticipatory feeding behavior in gulls is not new. Gulls have been reported to follow boats in anticipation of scavenging food scraps or discarded fish (Bent, 1921). They will congregate near waterfront restaurants waiting for garbage, or on fishing piers or docks in expectation of discarded fish or fish parts. The starting sound of the motor driving a conveyor belt outside a fish cannery attracts gulls before food appears (Frings *et al.*, 1955). Many gulls will remain near humans on a beach rather than feed on sparse, but available, food in the sea or in the wave-lap zone just a few meters away. The nature of such food identification has led one group of writers to remark on some coast dwellers' belief that gulls have a "sixth sense" (Frings *et. al.*, 1955). Although there are cueing differences, these birds also seem to have learned that such behavior will be rewarded.

Learning capacities are species specific in many cases. Eibl-Eibesfeldt

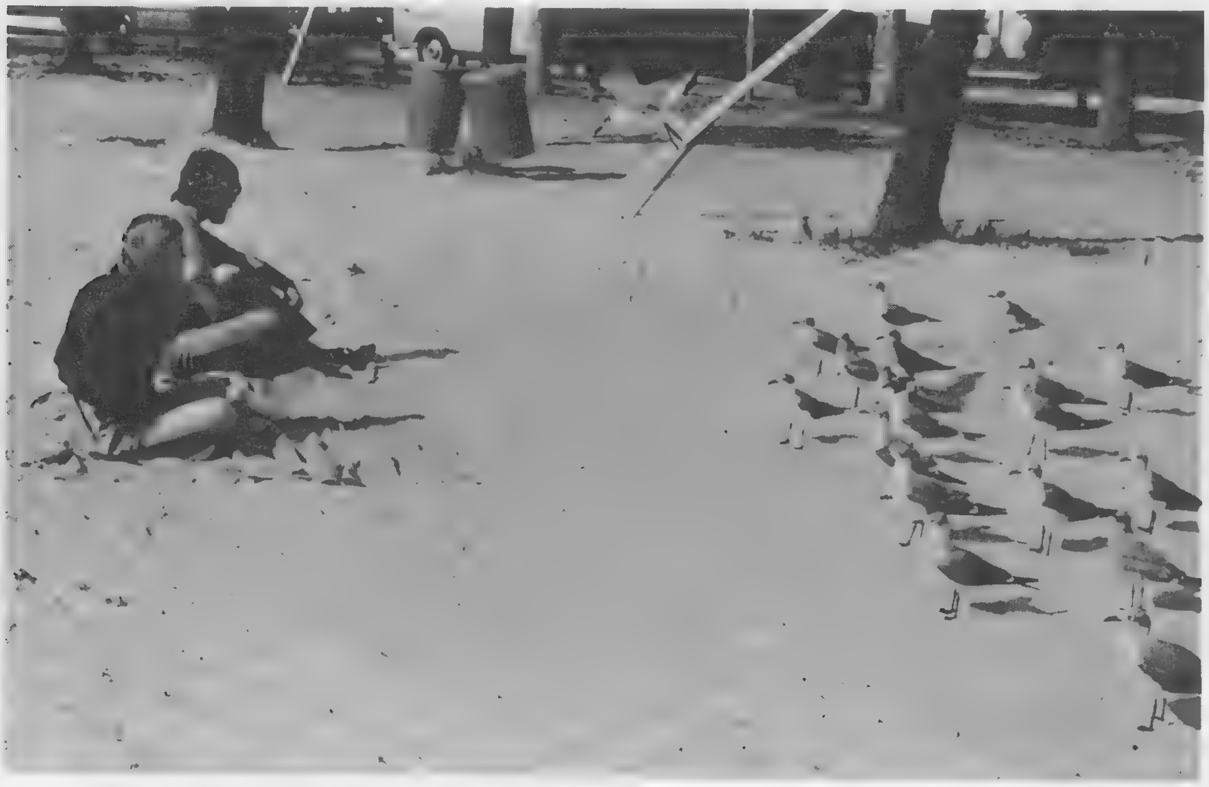

Figure 2. A defending gull (upper center) will occasionally take flight for a few seconds. At this time, some peripheral birds move closer. The defender chases the invaders back when he alights.

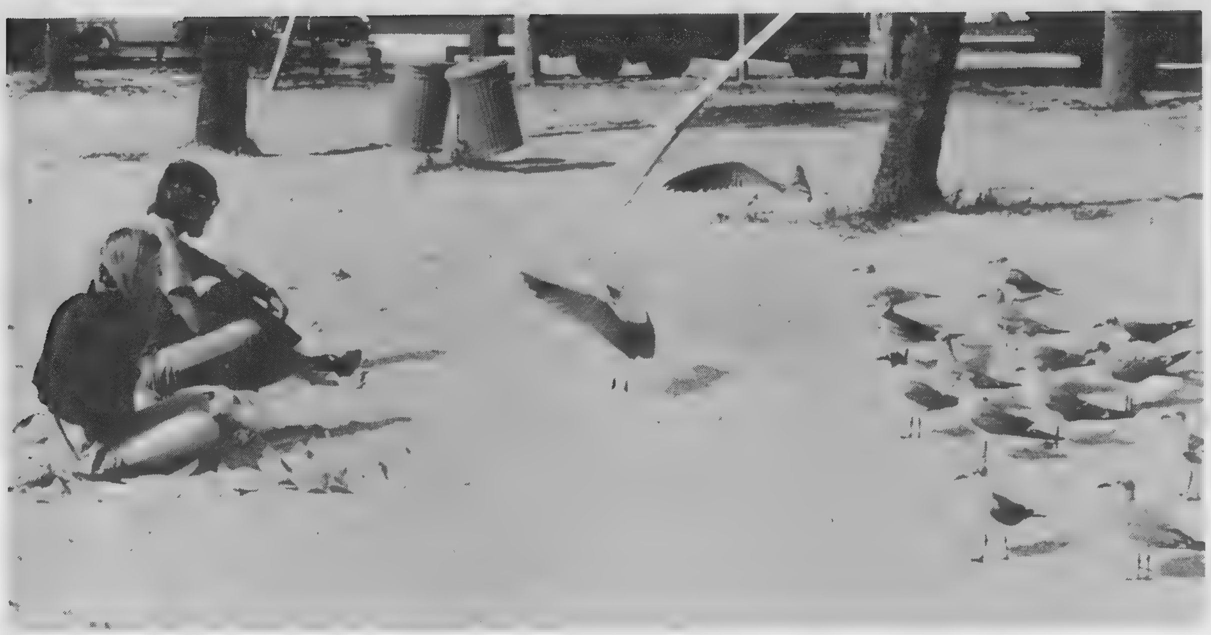

Figure 3. A defending gull (closest to people) has just driven off an invader (airborne). Other gulls stand behind the territorial boundary.

(1970) notes that predators are intelligent in matters dealing with the capture of prey and the learning of paths or trails used by prey. It seems reasonable to postulate that gulls, which spend a large percentage of their time and energy foraging, will exhibit analagous adaptations.

Local residents, who regularly feed airborne birds from the hand, reported to me that the birds have learned to identify food with a high degree of skill. Other writers also commented on the visual acuity of gulls (Frings *et al.,* 1955; Tinbergen, 1971). Common objects such as combs, bottle caps, and pens generally do not attract the birds. These discriminatory abilities appear to hold true for anticipatory behavior as well; some birds appear to have learned to recognize potential food sources. I observed gulls setting up territories only around persons with bags or bundles that might contain food.

Tinbergen (1960) noted that "the most obvious thing" about gulls' behavior is ". . . their lack of insight into the ends served by their activities and into the way their own behaviour serves these ends." Although all birds possess stereotyped actions in responding to certain stimuli, many species, including Laughing Gulls, possess behavioral plasticity when confronted by new and adaptively beneficial situations. In this case, man has provided the potential for modifying a behavioral rigidity that is generally functional and adaptive.

Territorial defense serves different functions in different animals, and territories need not be fixed in either space or time. Although many species of birds territorialize food supplies, feeding territories that float in space and time are more common among mammals that cannot constantly defend the larger geographic area required for food supply, or among animals that depend on mobile food sources. It is interesting to note, however, that territoriality in Herring Gulls is not uniform throughout the species. Depending on location, this gull can show a duality in behavior, exhibiting either territorial or colonial nesting strategy (Wynne-Edwards, 1962).

Many birds are fast learners, and learned information can travel rapidly. Fisher and Hinde (1949) documented the ability of novice titmice to open milk bottles to withdraw cream, after learning this ability from experienced individuals. Hinde and Fisher (1951) subsequently reported similar observations

TABLE 1

Establishment of Territory by Laughing Gulls

Defender	*Time required to set up territory*[1]	*Number of birds repelled*
1	1.25	3
2	2.0	2
3	2.0	2
4	2.5	5
5	2.75	4
6	2.75	5
7	3.25	6
8	3.5	7
9	3.75	9
10	4.0	3
11	4.0	12

[1] In minutes.

among titmice in several European countries.

It will be interesting to see whether this territorial behavior in Laughing Gulls (1) is sufficiently advantageous to be widely imitated, (2) is of marginal advantage and will appear only sporadically, or (3) if it will disappear.

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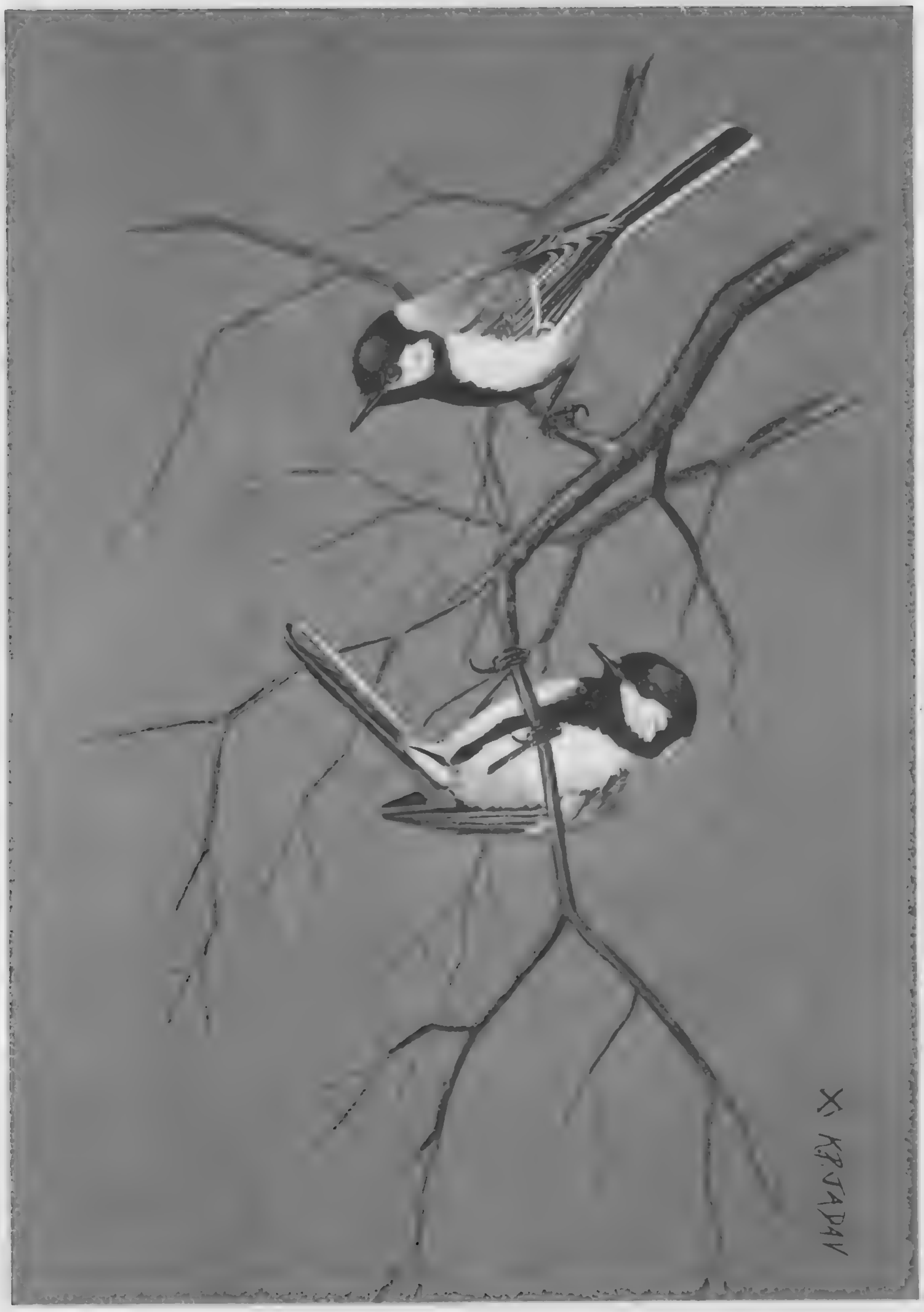


Grey Tit, *Parus major*. Painting by K. P. Jadav.

THE DEVELOPMENT OF FOUR NORTH AMERICAN HERONS. II

William McVaugh, Jr.

Paintings by the author

Knowing that little published information is available that documents the developmental stages of herons, I began gathering information some years ago, working first at Pea Island National Wildlife Refuge in North Carolina in 1968 and 1969. The results of this study appeared in *The Living Bird,* 1972, where I reported on the development of the Louisiana Heron *(Hydranassa tricolor),* Black-crowned Night Heron *(Nycticorax nycticorax),* Common Egret *(Casmerodius albus),* and Little Blue Heron *(Florida caerulea).*

In the study presented here, my aim is to document the development of the nestling herons by recording measurements, plumage changes, and color transformation of the unfeathered portions of the nestlings. The four species studied include the Green Heron *(Butorides virescens),* Snowy Egret *(Leucophoyx thula),* Yellow-crowned Night Heron *(Nyctanassa violacea),* and Least Bittern *(Ixobrychus exilis).* The study was carried out at St. Marks National Wildlife Refuge in Florida.

Nesting

The four species in the family Ardeidae studied at St. Marks nested in different situations. Green Herons nested over fresh water in black willows whose trunks and root systems were in, or adjacent to, water. Nests were usually relatively few and widely scattered, although five nests in 1972 were grouped together in a large clump of willows. I found only four Green Heron nests in 1973. One of these was later destroyed, probably by Boat-tailed Grackles.

Snowy Egrets nested with Louisiana and Little Blue Herons. They used the same rookery in 1972 and 1973, in spite of the fact that the black willows died after hurricane Agnes struck the area in June of 1972. The 1973 nests were exposed, and the lack of leaf protection may have caused the frequent nest abandonment that I observed. I recorded more missing and dead nestlings in 1973 than in 1972. The 1973 nests numbered about 75, of which 14 were tagged and studied. One Snowy Egret hatched in a nest containing two Louisiana Heron nestlings that hatched at approximately the same time. An adult pair of Louisiana Herons fed all three nestlings until they fledged.

Yellow-crowned Night Herons nested in a few titi trees on the edge of a cypress swamp. In 1972, the colony numbered 19 nests. The herons built 13 nests in 1973, laying 53 eggs, of which 44 hatched. The pairs built their nests from seven to 14 feet above the water.

Least Bitterns constructed nests along the edges of pools in fresh water cordgrass, sawgrass, and common cattails. Nests were placed within two feet of open water at the base of the grass or cattails. Adults usually scattered their nests, although I found two nests within 10 feet of each other. Dead and matted vegetation on the outer perimeter of the water areas provided excellent cover for fledglings. I found six nests in 1973. High water forced the abandonment of two of these; a predator destroyed another.

Methods

Site of Study

From 22 May to 30 June 1972 and 5 April to 19 June 1973 and 6 April to 29 June 1974, I collected field data at St. Marks National Wildlife Refuge in northwestern Florida on the shores of Apalachee Bay. The refuge's 65,000 acres contain salt and brackish marshes, hardwood swamps, pine flatlands, and pine-oak upland.

In my earlier paper in the 1972 *Living Bird,* I described my methods of approaching a colony of herons and working among them. I refer the reader to that article.

Sample Size and Frequency of Visits

I was in the colony each day to record measurements and changes in plumage and colors of unfeathered parts. My sample sizes for each of the species studied were: Green Heron, 19 nestlings; Least Bittern, 50 nestlings; Yellow-crowned Night Heron, 52 nestlings; Snowy Egret, 37 nestlings. I recorded data on each nestling every day, or up to every five days.

Marking Nests and Young

I identified each nest being studied with a data tag enclosed in a plastic bag and fastened near the nest. To the tag, I added information as the nesting cycle proceeded. I banded each nestling to establish its identity. Since the tarsus of a newly hatched heron is usually too small to retain a band, I found some identifying mark on each nestling to support the information I recorded until the tarsus was large enough to hold a band.

I removed each heron from its nest and photographed, sketched, and measured it, and recorded plumage and color changes.

Kinds of Data Collected

All descriptive information reflects the appearance of young birds hatched and reared in a specific locality, and does not necessarily hold true for populations elsewhere.

I photographed and measured the nest and eggs for each species, and noted any unusual nesting condition. When eggs hatched, and periodically thereafter, I photographed young of known ages, described the colors of the unfeathered, or soft, parts, and recorded linear measurements of bill, body, wing, secondary and primary feathers, tail, tarsus, and middle toe.

For one-day-old nestlings, I recorded minimum and maximum measurements. After the first day, the growth rate tended to vary more between nestlings of the same age, the variation depending upon the available food supply, the rate of parental feeding, and aggressiveness of the young.

In addition to recording colors, behavior, and measurements, I made sketches of the birds and, as the young developed, recorded an increasing number of topographic and physical features—from 29 to 67—for each nestling. I banded each nestling with a U.S. Fish and Wildlife Service band for positive identification.

The color terminology, for the sake of simplicity, is based on the seven prismatic spectrum-color divisions and their intermediate values, plus black and white. I used other color terms, such as ivory, tawny, flesh, horn, and dusky, and described a body area with a singular or binomial color name—e.g., green or blue-green. Since any hue varies with intensity, I used modifiers such as pale, light, medium, and dark.

My statements on plumage are based on the average appearance and characteristics exhibited by a specific age group. I noted the emergence of the juvenal plumage and measured specific primaries and secondaries, the flight feathers of the wing, and rectrices, the flight feathers of the tail. When the young bird became more or less covered with feathers, I measured only the flight feathers in most cases. I described the color of the bare skin as long as it was visible.

Measurements

For those interested in knowing how I made my measurements, I mention below my methods, which are largely those described in "Measurements of Birds" by S. P. Baldwin, H. C. Oberholser, and L. G. Worley (Sci. Publ. Cleveland Mus. Nat. Hist., 2:1-165, 1931). All measurements are shown in millimeters.

Body length: from the tip of the bill to the tip of the longest rectrix with neck extended and the bird on its back.

Wing length (hand): from the distal bend of the wing, or wrist, marked by the junction of the forearm with the hand, to the tip of the hand excluding the feathers until the feathers emerge, at which time the length becomes the wing chord from the bend of the wing (wrist) to the tip of the longest primary.

Wing length (extended): measured across both extended wings from tip to tip.

Bill: the upper mandible from the base of the exposed culmen, the upper ridge, in a straight line to its tip.

Tail: the longest rectrix from its insertion in the follicle to its tip.

Tarsus: from the middle of the joint between the tibiotarsus and the tarsometatarsus behind to the lower edge of the lowest undivided scute on the front of the junction of the tarsometatarsus with the base of the middle toe.

Middle toe: from the junction of the middle toe with the foot to the distal end of the toe, excluding the nail.

Developmental Stages

Descriptions and illustrations of the various developmental stages of four species of North American herons follow. For descriptions of color and size of eggs, I refer to A. C. Bent's "Life Histories of North American Marsh Birds" (U.S. Natl. Mus. Bull. 135, 1926), C. A. Reed's "North American Birds Eggs" (Doubleday, Page and Company, New York, 1904), and Palmer's "Handbook of North American Birds," volume 1 (Yale University Press, New Haven, 1962). For anatomical terms, I followed "Ornithology in Laboratory and Field" by O. S. Pettingill, Jr. (Burgess Publishing Company, Minneapolis, 1970).

GREEN HERON

Eggs

Females usually lay four to five eggs, ovate or oval in shape, and pale greenish or bluish green in color.

Age One Day

Plumage

Head, neck, wings, and back covered with long medium gray down, up to 19.1 mm, darker gray on head and mixed on neck and wings. Pale gray to white on breast, abdomen, and wings.

Unfeathered Parts

Skin of forehead and crown fleshy pink, pale green around the eyes to greenish blue near the crown. Auricular area pink. Neck dorsally from head to body greenish; body dorsally greenish; breast and abdomen flesh color, anal region greenish. Upper mandible pale greenish gray proximally, culmen dark pinkish gray to black distally, tip black, rounded sides of bill pinkish, nostril arch paler; black line runs just above the cutting edge from the commissural point to about one-half the length of the bill; egg tooth present; lower mandible with rounded sides pinkish to black distally and small ivory tip. Mouth lining pale pink. Iris pale gray—off-white in some nestlings; eye-ring pale green. Top of tarsus greenish flesh to flesh; heel and bottom of tarsus pale flesh; toes flesh above, pale flesh below; under-toes pale flesh; nails ivory.

Measurements

Body. length 95.3 mm; wing 15.9 mm; bill 12.7 mm; tarsus 15.9 mm.

Age Three Days

Plumage

Head, neck, wings, and back covered with dark gray down, up to 19.1 mm on the forehead; down on the forehead pale gray, under neck and breast pale gray; abdomen and femoral areas white. No emergence of quills.

Unfeathered Parts

Skin of head flesh color; skin around eyes bluish gray blending to yellowish green; neck greenish; wings and body pale greenish to flesh color; abdominal area pale grayish green to darker around anal area. Upper mandible yellowish pink blending to black at tip; distal one half of cutting edge black; egg tooth present. Sides of lower mandible yellowish proximally to pinkish distally blending to black near tip; small ivory tip. Mouth lining pale pink. Iris pale gray to off-white; eye-ring pale yellow-green. Tarsus and toes pale yellow above and below; nails pale bluish gray with paler tips.

Measurements

Body length 108 mm; wing 19.1 mm; bill 15.9 mm; tarsus 20.6 mm; middle toe 23.8 mm.

Age Six Days

Plumage

Head, neck, and back covered with medium gray down, up to 19.1 mm on the forehead and crown; under neck, breast, abdominal, and femoral regions pale gray to white. Quills, down-tipped, emerging from all feather tracts except crown and tail. All secondary covert quills emerging, down tipped.

Unfeathered Parts

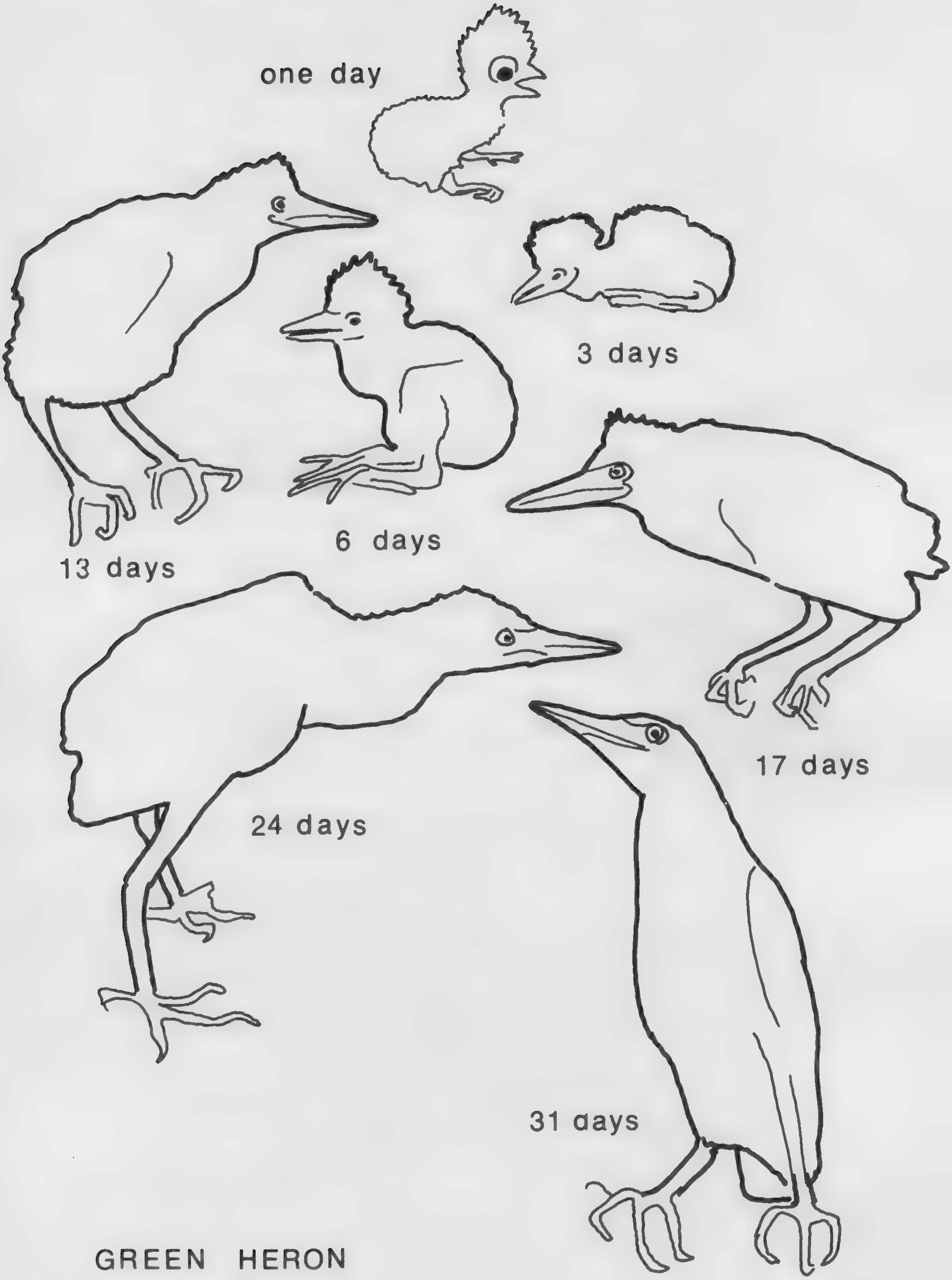
Skin of forehead and crown pinkish, auricular area greenish; yellow-green skin around the eye blends to pale greenish blue over the eye; neck and body pale yellow-green, abdominal areas pale gray-green to deep gray-green in anal region. Upper mandible pinkish yellow proximally, nostril arch paler; culmen darker merging to a black tip; tomium and distal one-third of mandible dark; egg tooth present. Lower mandible pinkish yellow proximally, changing from pink to black distally with an ivory tip. Mouth lining pale pink. Iris pale gray to off-white, eye-ring pale green. Tarsus and toes pale yellow-green, toes lighter; heel and underside of tarsus yellow; nails pale ivory.

Measurements

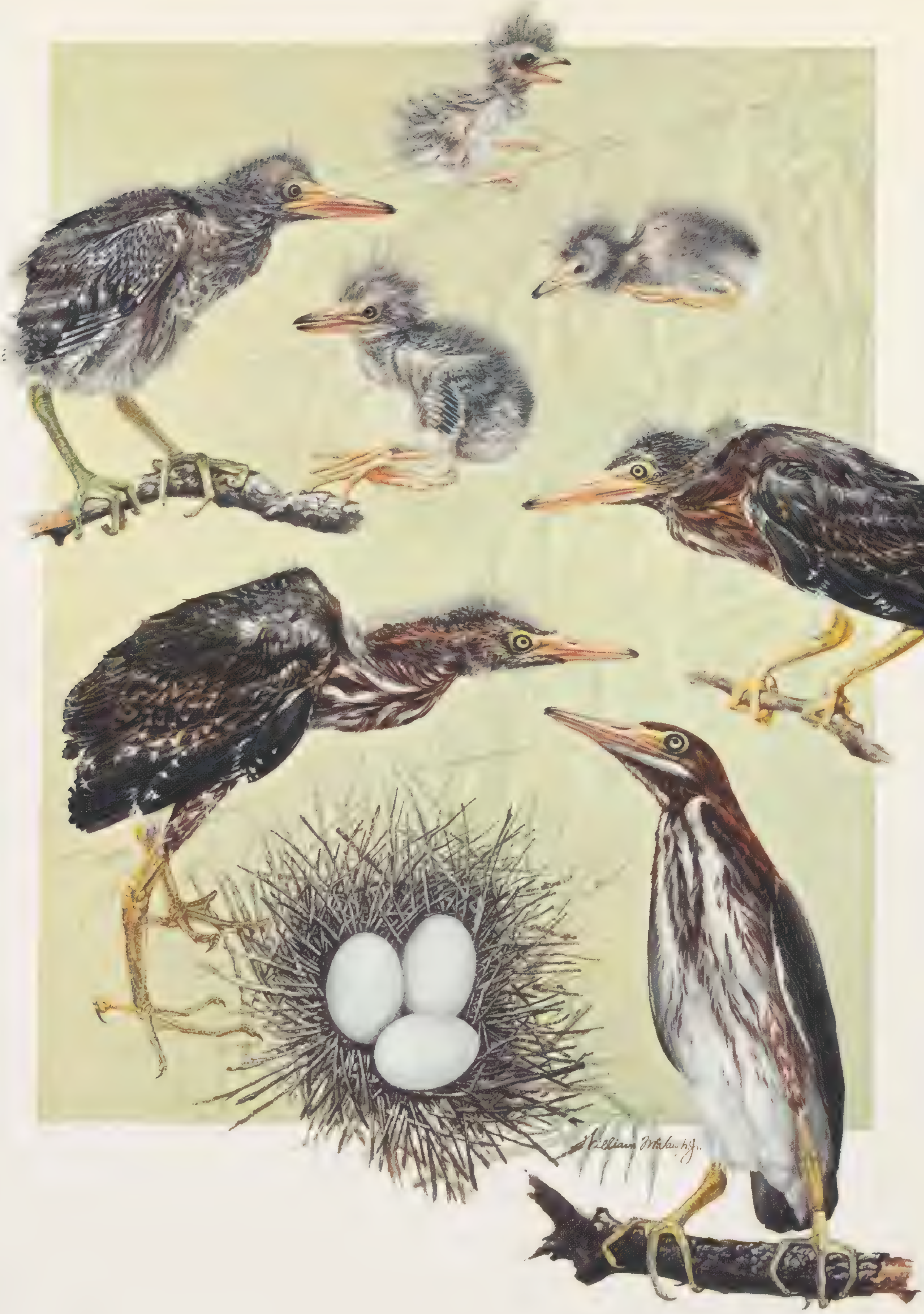
Body length 184.2 mm; wing 25.4 mm; bill 19.1 mm; tarsus 30.2 mm; middle toe 31.8 mm; longest primary pinfeather 9.5 mm; longest secondary pinfeather 9.5 mm; longest scapular pinfeather 9.5 mm.

Age Eight Days

The body description remains the same as age six days. All quills have increased in length approximately 30 percent; crown and tail quills just emerging.



GREEN HERON


William

Age Eleven Days

Plumage

Quills emerging on all feather tracts; dark gray down remains on head and neck, gray down on all emerging feathers. Emerging juvenal feathers on wings and back very deep gray—almost black; primary and secondary coverts emerging; juvenal feathers emerging on neck, breast, and abdomen. Emerging primaries, secondaries, and primary coverts are black, tipped with white; secondary coverts black with reddish brown tips; mantle dark gray with reddish sheen; emerging feathers on front of neck and breast pale brown; soft white down-like feathers on the abdomen; femoral tract feathers medium gray. Crown and tail quills tipped with down.

Unfeathered Parts

Skin of forehead and crown bright yellowish green; lores yellow; neck and back yellowish green, back deeper green towards the tail; breast and abdomen pale green, deeper near the tail; skin around eye yellow to greenish yellow (some individuals), deeper greenish over the eye. Upper mandible greenish orange, more greenish proximally; nostril arch paler; culmen pale orange; black tip; cutting edge black distally. Lower mandible greenish orange proximally, paler orange distally changing to black; pale ivory tip. Mouth lining pale pink to pink. Iris grayish white to off-white; eye-ring pale green. Top of tarsus pale green—yellow-green in some; heel and under-tarsus yellow; toes darker green than tarsus above, deep yellow below; nails medium gray with pale tips. Scales formed on tarsus and toes.

Measurements

Body length 222.3 mm; wing chord 38.1 mm; bill 27.0 mm; tarsus 46.0 mm; middle toe 46.0 mm; length of emergence from sheath of fifth primary 9.5 mm; emergence of fifth secondary 9.5 mm; emergence of longest scapular 12.7 mm.

Age Thirteen Days

Plumage

Quills emerging on head and neck, grayish down on head, neck, and back, longest (15.87 mm) on forehead. Juvenal feathers of rump just emerging; mantle feathers deep gray with greenish sheen; primary and secondary feathers and primary coverts black with white tips; secondary coverts black with greenish sheen; median coverts black with medium to dark reddish brown V-shaped tips; lesser coverts black edged in reddish brown; emerging ventral neck feathers reddish brown and reddish gray; partly emerged breast feathers dark gray with light brown tips, each feather broadly streaked with a pale gray or white median stripe; abdominal feathers white. Gray down still attached to most contour feathers.

Unfeathered Parts

Quills and feathers cover most of the body; lores yellow to greenish yellow; skin of neck, breast, and abdomen pale green, darker near the tail. Upper mandible pale greenish orange proximally, rounded sides orange, tip black; nostril arch and culmen pale orange; cutting edge black distally; egg tooth present. Lower mandible orange blending to black distally; tip, pale ivory. Mouth lining pale pink to pink. Iris grayish white, pupil black; eye-ring yellowish green. Top of tarsus pale green, yellow below; toes darker green above, deep yellow below; nails pale horn. Scales well formed on tarsi and toes.

Measurements

Body length 245.0 mm; wing 85.7 mm; bill 44.5 mm; tarsus 49.2 mm; middle toe 50.8 mm; length of emergence from sheath of fifth primary 14.3 mm; emergence of fifth secondary 15.9 mm; emergence of longest rectrix 3.2 mm; emergence of longest scapular 12.7 mm.

Age Seventeen Days

Plumage

Head, neck, and body covered with emerging feathers; down still attached to most feathers, especially on head, neck, and mantle, and longest (15.87 mm) on forehead and crown. Primary and secondary feathers black with greenish sheen; white tipping and edging on the primaries and secondaries, mostly on the outer vane; greater, median, and lesser coverts black with small white V-shaped tips; outer vane of greater secondary coverts edged with pale buff; median coverts with outer vane edged in buff; lesser coverts edged with reddish brown; all coverts have a greenish sheen, the lesser coverts have an intermixture of greenish and reddish sheen. Tail feathers black with greenish sheen; ventral neck feathers pale brownish gray with a dark brown median streak, neck stripe white; breast feathers pale gray streaked with white and tipped in buff; feathers of abdomen white with pale gray and buff streaks.

Unfeathered Parts

Lores and rictus yellow to greenish yellow. Upper mandible with orange sides; culmen and nostril arch paler; cutting edge dark blending to black tip; egg tooth present. Lower mandible orange proximally to black distally; small ivory tip. Mouth lining pale pink. Iris yellowish white; eye-ring greenish yellow. Top of tarsus pale greenish yellow, orange-yellow to yellow below; toes darker greenish yellow above, orange below; nails medium horn, tips paler; web between second and third toes orange to orange-green. Scales well formed on tarsi and toes.

Measurements

Body length 317.5 mm; wing 117.5 mm flattened; bill 36.5 mm; tarsus 28.6 mm; middle toe 44.5 mm; length of emergence from sheath of fifth primary 41.3 mm; emergence of fifth secondary 31.8 mm; emergence of longest rectrix 17.5 mm.

Age Twenty-four Days

Plumage

Head and neck covered with emerging feathers; body covered with juvenal feathers; brownish gray down on forehead and crown, longest (19.05 mm) on crown; some down on body. Emerging head feathers black; neck feathers reddish brown; primary feathers black with greenish sheen; small triangular white spots and white edging on the proximal part of the outer vane blending into the white tip; secondaries black with greenish sheen and small white tips; greater primary coverts black with greenish sheen and small white triangular spots; greater secondary coverts brownish black with greenish sheen and small triangular spots, edging of outer vane pale buff gradually darkening to reddish brown in coverts near the tertiaries; median coverts blackish brown with green sheen, elongated V-shaped spots off-white to pale buff to reddish; lesser and marginal coverts blackish brown edged and V-tipped in reddish brown; some gray down on tips of coverts; mantle, scapular, and back feathers dark brown; rectrices black with greenish sheen; feathers on side of neck white (inner vane and shaft) and, dark brown (outer vane); ventral neck feathers white with dark brown median streak; breast feathers dark brown with white shaft and buffy median streak; abdominal feathers white with dark brown median streak, and edged in gray towards the tail; under-tail coverts buffy white.

Unfeathered Parts

Lores and rictus yellow to greenish yellow. Upper mandible orange, distal end black with small ivory tip. Lower mandible orange blending to pale orange distally; small black tip. Mouth lining pale pink. Iris greenish white to yellowish white; eye-ring greenish yellow to greenish blue. Tarsus pale yellowish green (some grayish green) above, yellow to pale yellow below; toes grayish green dorsally, pale orange yellow ventrally; nails medium horn, dark tips.

Measurements

Body length 323.9 mm; wing 130.1 mm; bill 41.3 mm; tail 49.2 mm; tarsus 49.2 mm;

middle toe 44.5 mm; length of emergence from sheath of fifth primary 63.5 mm; emergence of fifth secondary 54.0 mm; emergence of longest rectrix 19.0 mm.

Age Thirty-One Days

Plumage

Entire body well covered with juvenal feathers; sparse gray down attached to some wing and body feathers; forehead and crown black; neck reddish brown dorsally; scapular region and back dark reddish brown to dark brown; tail black with greenish sheen. Primaries black with greenish sheen, with small triangular white spots and white edging on the lower part of the outer vane blending to a white tip; primary coverts black with greenish sheen and small triangular white spots at the tip; secondaries black with greenish sheen and small white tips; secondary coverts brownish black with greenish sheen, with small triangular buffy white spots; outer vane edged in pale buff, the feather edging darkening to reddish brown near the tertials; median coverts blackish brown with greenish sheen, with elongated V-shaped off-white to pale buff to reddish buff spots; lesser and marginal coverts blackish brown, edged and V-tipped in reddish brown; neck white with reddish to dark brown streaking ventrally; breast white with buff streaking, some dark brown streaking extending into the white abdomen; under-tail coverts buffy white to white.

Unfeathered Parts

Bare lores yellow to greenish yellow. Upper mandible orange, black distally with small ivory tip. Lower mandible orange blending to pale orange distally; tip black. Mouth lining pale pink. Iris greenish white to yellowish white in some; eye-ring greenish yellow to greenish blue. Tarsus yellow-green to grayish green above, yellow to pale yellow below; toes grayish green above, pale yellow to pale orange-yellow below; nails medium horn.

Measurements

Body length 330.2 mm; wing 142.9 mm; tail 60.3 mm; bill 46.0 mm; tarsus 57.2 mm; middle toe 46.0 mm; length of emergence from sheath of fifth primary 85.7 mm; emergence of fifth secondary 76.2 mm; emergence of longest rectrix 20.6 mm.

LEAST BITTERN

Eggs

Females usually lay four to five eggs, elliptical in shape, and pale bluish or greenish in color.

Age One Day

Plumage

Head, neck, and back covered with pale buff down, longest (12.70 mm) on forehead and crown; chin, neck (ventrally), and femoral region covered with white down. Down on chicks in different nests varies in color from pale buff to deep buff; all nest-mates are either pale, medium, or deep buff-colored with no intermixture of intensity.

Unfeathered Parts

Head, neck, and back pinkish, forehead darker; neck yellowish ventrally; abdominal area greenish, darker around the cloacal region; humeral region pink; skin around the eyes grayish blue, darker above the eyes; auricular area pink. Upper mandible pinkish yellow, blending distally to a black tip; nostril arch more yellowish; distal half of tomium black; egg tooth present. Lower mandible yellowish pink proximally, blending to black distally; small amber tip. Mouth lining pink to deep pink. Iris off-white; eye-ring pale gray. Tarsus pinkish flesh above, pale yellow below; toes pale pinkish flesh above, pale yellowish gray below; nails pinkish ivory.

Measurements

Body length 76.2 mm; wing 10.3 mm; bill 10.3 mm; tarsus 12.7 mm; middle toe 11.9 mm.

Age Five Days

Plumage

Head, neck, and back covered with pale buff down. All nest-mates are either light, medium, or deep buff in color with the same intensity—no lighter or darker chicks in the same nest. Longest down filaments (12.70 mm) on the forehead and crown. Chin, ventral neck, and femoral regions covered with white down. Scapular quills first to appear (3.18 mm), tipped with down.

Unfeathered Parts

Head and neck pinkish flesh, forehead and back pinkish blue; skin around the eye pale gray-blue, auricular area pink; neck flesh color; abdominal region dark grayish purple; rest of ventral area greenish blue. Upper mandible bluish proximally, rounded sides and nostril arch pale flesh color; distal end pinkish brown; tip black; egg tooth present. Lower mandible pale blue proximally to pinkish flesh to black distally with small ivory tip. Mouth lining pale pink. Iris off-white; eye-ring pale gray. Tarsus pinkish above, yellow to pale yellow below; toes flesh color above, pale yellow-gray below. Nails pale pinkish gray with lighter tips.

Measurements

Body length 120.7 mm; wing 17.5 mm; bill 15.9 mm; tarsus 22.2 mm; middle toe 22.2 mm.

Age Seven Days

Plumage

Head, neck, and body covered with down, longest filaments (12.70 mm) on the forehead and crown. White down on ventral neck and abdominal region.

Unfeathered Parts

Forehead and crown dark grayish pink; top of neck deep pink; under-neck and breast pink; abdominal region purplish green; skin around eyes bluish green, deeper over the eyes; lores pale bluish. Upper mandible pale greenish proximally blending to flesh color to brownish distally; culmen and nostril arch deep flesh color; tip black; egg tooth present. Lower mandible pale purplish proximally, deeper distally to black end with small ivory tip. Mouth lining pale to deep pink. Iris pale gray, eye-ring gray. Tarsus grayish yellow above, pale yellowish below; top of toes yellow, deeper near the nails, pale yellowish below; nails bluish gray with pale tips.

Measurements

Body length 139.7 mm; wing 22.2 mm; bill 19.0 mm; tarsus 28.6 mm; middle toe 30.2 mm; longest primary pinfeather 9.5 mm; longest secondary pinfeather 9.5 mm; longest scapular pinfeather 6.4 mm.

Age Eight Days

Plumage

Head, neck, and body covered with medium buff down, longest (12.70 mm) on the forehead and crown. Some vanes emerging from quills. Emerging scapulars are black with reddish brown tips; mantle feathers black; upper abdominal feathers pale buff, lower abdominal feathers white.

Unfeathered Parts

Head, neck, and body greenish flesh; skin around eyes pale green, pale blue in some; abdomen grayish flesh; lores greenish pink to pink. Upper mandible pinkish with pinkish gray culmen proximally, darker distally; black tip; nostril arch flesh color; egg tooth present. Lower mandible greenish pink proximally, darker distally to black terminus with small ivory tip. Mouth lining pale pink to pink. Iris pale gray to deeper gray in some individuals, eye-ring pale blue to yellowish green. Tarsus yellowish green above, yellow below; toes yellow above, pale yellow-gray below; nails pinkish gray with pale tips.

Measurements

Body length 177.8 mm; wing 28.6 mm; bill 25.4 mm; tarsus 28.6 mm; middle toe 36.5 mm; longest primary pinfeather 12.7 mm; longest secondary pinfeather 12.7 mm; longest scapular pinfeather 12.7 mm.

Age Twelve Days

Plumage

Emerging crown quills down-tipped; nape quills brown, also down-tipped. Pale down covers most of the head, neck, and body, longest on the forehead and crown. Emerging primaries and secondaries brown, tipped with down, feathers of back dark gray to black, edged and tipped in pale brown to reddish brown; greater and median coverts tipped with pale brown down; lesser coverts are down-tipped pinfeathers; rump feathers emerging; ventral neck feathers white with buff streaks; upper breast feathers pale buff; abdominal feathers white; crural feathers white with long down filaments attached.

Unfeathered Parts

Skin around eyes pale green; lores pale greenish yellow; abdominal skin pale flesh color. Upper mandible greenish flesh blending to black tip; culmen dark pinkish grey, darker distally; egg tooth present. Lower mandible greenish proximally, blending to pale pink, turning darker distally to small black spot; pale ivory tip. Mouth lining pale pink. Iris gray; eye-ring yellow-green to yellow. Tarsus gray-green above, yellow below; toes gray-green to gray-yellow above, pale yellow-gray below; nails gray with pale tips. Scales well formed on tarsi and toes.

Measurements

Body length 190.5 mm; wing 38.1 mm; bill 22.2 mm; tail 9.5 mm; tarsus 38.1 mm; middle toe 38.1 mm; longest primary pinfeather 19.1 mm; longest secondary pinfeather 19.1 mm.

Age Thirteen Days

Plumage

Feathers emerging on all feather tracts; forehead, crown, and nape covered with pale buff down, longest (19.05 mm) on the forehead; pale buff down on wings and body, heavy on the spinal tract and lower back; pale buff to white down on ventral neck and abdominal area. Primaries and secondaries black, outer vane tipped and edged in reddish brown; greater primary coverts black with reddish brown tips; greater secondary coverts reddish brown; median and lesser coverts paler reddish brown; marginal coverts not emerged; scapulars and feathers of back black with reddish sheen, edged in reddish brown; neck feathers near the crown pale reddish brown; ventral neck feathers an intermixture of pale buff, white, and dark reddish brown; breast feathers pale buff; abdominal feathers pale gray to white; under-tail coverts white.

Unfeathered Parts

Skin around eyes pale blue to greenish blue; lores pale greenish yellow. Upper mandible pale pinkish to pale greenish proximally, darker distally; ivory tip; egg tooth present. Lower mandible greenish to pinkish proximally, darker distally; small ivory tip. Mouth lining pale pink. Iris gray; eye-ring pale blue to pale bluish green. Tarsus pale gray-green above, pale yellow below; toes above pale gray-green blending to pale yellow near nails, pale yellow to yellow below; nails gray with pale tips.

Measurements

Body length 165.1 mm; wing 53.9 mm; bill 27.0 mm; tarsus 34.9 mm; middle toe 38.1 mm; length of emergence from sheath of fifth primary 4.7 mm; emergence of fifth secondary 4.7 mm; emergence of longest scapular 12.7 mm; rectrices just breaking sheaths.

Age Seventeen Days

Plumage

Pale buff down attached to emerging feathers on the head, neck, wings, back, and tail; white down attached to breast, abdomen, and flank feathers; forehead and crown feathers black, auricular area reddish brown; top of neck reddish brown to dark gray; scapulars dark gray, tipped with reddish brown; back dark reddish brown to dark reddish gray; tail feathers deep gray. Primaries deep gray, numbers 1, 2, and 3 with reddish brown tipping; secondaries deep gray with reddish brown tipping; primary coverts deep gray with deep reddish brown tipping; secondary coverts deep reddish brown; median coverts pale reddish brown; lesser coverts pale buffy tan with dark gray at the base of the shaft; marginal coverts not emerged; throat feathers white with reddish buff streaking; upper breast very pale buff blending to white; lower breast and abdomen white; flank feathers white with gray at the base of the shaft; under tail coverts white.

Unfeathered Parts

Skin around eyes pale green blending to pale blue; lores pale greenish yellow to pale yellow. Upper mandible with pale pinkish gray culmen proximally, darker distally; dark tip; nostril arch pale green to pinkish green; rounded sides pale green proximally blending to pinkish green to darker distally. Lower mandible, rounded sides pale pinkish gray proximally to darker distally. Mouth lining pale pink. Iris off-white; eye-ring pale blue. Tarsus pale green above, heel and ventral tarsus pale yellow; toes yellow-green, pale yellow below; nails gray, pale tips.

Measurements

Body length 222.3 mm; wing 73.0 mm; tail 19.1 mm; bill 28.6 mm; tarsus 38.1 mm; middle toe 39.7 mm; length of emergence from sheath of fifth primary 19.1 mm; emergence of fifth secondary 11.1 mm; emergence of longest rectrix 4.8 mm.

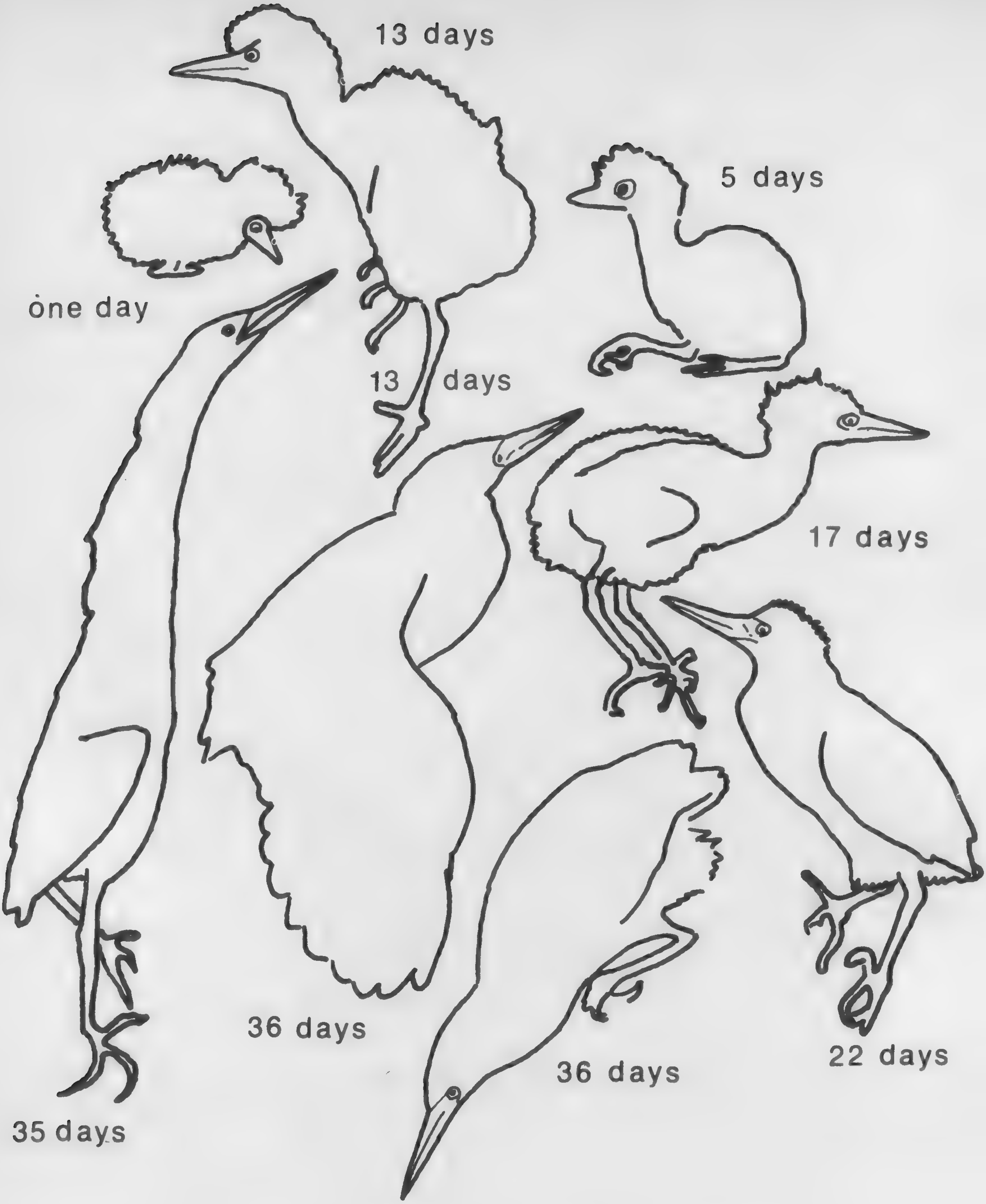
Age Twenty-Two Days

Plumage

Pale buffy down attached to juvenal feathers on the forehead and crown and extending to the nape; forehead and crown feathers black; auriculars reddish brown; scapulars dark gray to grayish brown; back dark reddish brown; some down remaining on the back and wing feathers; tail feathers deep gray to black. Primaries black with reddish brown tips; secondaries black with reddish brown tips; primary coverts black with reddish brown tips; secondary coverts reddish brown; median and lesser coverts reddish brown to buffy red; marginal coverts emerging. Throat feathers white with buffy streaking; breast feathers pale buff to white on the abdomen; under-tail coverts white.

Unfeathered Parts

Skin around eyes pale green to pale blue; lores pale greenish yellow to pale yellow. Upper mandible with pinkish gray culmen proximally to darker distally; dark tip; nostril arch pink; rounded sides pale pinkish green proximally blending to pink to dark grayish pink distally. Lower mandible pale pinkish gray proximally to darker distally. Mouth lining pale pink. Iris



LEAST BITTERN

off-white; eye-ring pale blue. Tarsus pale green above, pale yellow below; heel pale yellow; toes pale green above, pale yellow below; nails gray.

Measurements

Body length 254.0 mm; wing 92.1 mm; tail 27.0 mm; bill 34.9 mm; tarsus 39.7 mm; middle toe 39.7 mm; length of emergence from sheath of fifth primary 38.1 mm; emergence of fifth secondary 31.8 mm; emergence of longest rectrix 15.9 mm.

Age Thirty Days

Plumage

Heavy covering of pale buffy down remains attached to the head; some down on the neck; sparse down filaments on the upper back, wing coverts, rump, and upper tail coverts. Feathers on the forehead deep brownish black blending to deep reddish brown on the crown; auricular area buffy brown; upper neck reddish brown; scapulars black with pale buff to white tipping; upper back deep gray to reddish brown; back and rump dark reddish brown tipped in buffy to pale gray; upper tail coverts dark gray; tail feathers black. Primaries black, numbers one to six with V-shaped terminal spots of reddish brown, largest on the first primary, diminishing in size to a very small spot on the sixth; no spots on the remaining primaries; primary coverts black with two reddish brown spots on the outer vane, the spots merging on the inner vane; secondaries black with more or less triangular reddish brown spots on the tips; the last four secondaries adjacent to the tertials have a black inner vane; outer vane reddish brown; secondary coverts reddish brown; median and lesser coverts buff to reddish brown with a center stripe of dusky gray; marginal coverts white to buffy white; alula black with reddish brown tips. Throat feathers white with a narrow buffy edging flecked with fine black streaking to form a line terminating at the upper breast; neck with seven alternating stripes ventrally, buffy and brownish buff edged in white; side of neck buffy red; breast and abdomen white with feathers pale, tipped in pale buff to buffy red; sides and flanks white with buffy tips; under-tail coverts white.

Unfeathered Parts

Skin around eyes pale blue; lores pale gray to yellow-gray. Upper mandible with dark pinkish gray culmen proximally blending to deep gray (almost black) distally; nostril arch pale pink to grayish pink; sides of mandible pale green to pink proximally blending to deep pinkish gray distally; tomium dark pinkish gray. Lower mandible grayish pink, slightly deeper distally. Mouth lining pale pink. Iris pale yellowish white to white; eye-ring pale blue. Tarsus pale green to gray-green above, pale yellow to pale green below; toes grayish green above, pale gray below; nails pale to medium horn.

Measurements

Body length 304.8 mm; wing 114.3 mm; tail 34.9 mm; bill 39.7 mm; tarsus 39.7 mm; middle toe 39.7 mm; length of emergence from sheath of fifth primary 63.5 mm; emergence of fifth secondary 50.4 mm; emergence of longest rectrix 31.8 mm.

Age Thirty-Five Days

Plumage

Some pale buff down filaments remaining on the head and upper neck. Feathers on the head black; auricular area deep brown to buffy brown; top of the neck reddish brown, side buffy brown; scapular feathers black; mantle feathers deep gray with reddish brown tips; back and rump feathers dark reddish brown tipped in buffy gray to pale gray; upper tail coverts dark gray; tail feathers black. Primary feathers black with V-shaped reddish brown terminal spots; primary coverts black with reddish brown tips. Secondary feathers black with reddish brown tips, the last four feathers adjacent to the tertials—inner vane black, outer vane reddish brown; secondary coverts reddish brown; median and lesser coverts reddish brown; marginal coverts buffy white; alula feathers black with reddish brown tips. Throat and under-neck feathers white streaked with seven buff to buffy red stripes; side of neck buffy brown from auricular area blending to buffy red at the breast; breast and abdomen white with buffy red tipping; side and flank white with buffy red tipping; under-tail coverts white.

Unfeathered Parts

Skin around the eyes pale blue; lores pale gray to yellow gray. Upper mandible with dark pinkish gray culmen proximally blending to deep gray (almost black) distally; nostril arch pale to medium pink; sides of mandible pale greenish pink proximally blending to deep pinkish gray distally; tomium dark pinkish gray. Lower mandible grayish pink, slightly darker distally. Mouth lining pale pink. Iris pale grayish white or yellow-white to white; eye-ring pale blue. Tarsus pale grayish green above, pale to medium yellow below; heel medium yellow; toes gray-green above, pale gray below, nails medium horn.

Measurements

Body length 317.5 mm; wing 120.7 mm; tail 41.3 mm bill 39.7 mm; tarsus 39.7 mm middle toe 39.7 mm; length of emergence from sheath of fifth primary 69.9 mm; emergence of fifth secondary 57.2 mm; emergence of longest rectrix 38.1 mm.

YELLOW-CROWNED NIGHT HERON

Eggs

Females usually lay two to four eggs, nearly elliptical in shape, and pale bluish green in color.

Age One Day

Plumage

Head, neck, and body covered with long white or pale to medium gray down, longest filaments (34.92 mm) on the forehead and crown. Down on the head white, gray to dark gray at the base; body down white or gray, appears darker on some nestlings due to the darker gray color at the base of each feather.

Unfeathered Parts

Head pinkish gray; neck yellowish pink dorsally; wings and back flesh color to pinkish gray, darker on the rump. Neck pinkish ventrally; abdominal area pinkish yellow to yellow. The skin color of some nestlings varies slightly, both paler and darker than described above. Skin around the eye deep grayish blue blending to pale blue; auricular region flesh color. Upper mandible pinkish gray, pinkish yellow, or grayish yellow—lighter proximally, darker distally; culmen dark pinkish gray proximally, darker distally; nostril arch pale yellow to pinkish yellow; tip dark pinkish gray; small ivory tip; egg tooth present; cutting edge pale gray. Lower mandible pale yellow proximally to pinkish yellow distally; small ivory tip. Some chicks have paler upper and lower mandibles. Mouth lining pale pink. Iris pale yellow; eye-ring pale gray. Top of tarsus pale flesh to pinkish; some tarsi deep pinkish flesh; heel and under-side paler; toes pale flesh to pale pinkish; nails pale ivory.

Measurements

Body length 104.8 mm; wing 16.6 mm; bill 11.1 mm; tarsus 17.5 mm; middle toe 14.3 mm.

Age Five Days

Plumage

Head, neck, wings, and body covered with down, longest filaments vary from 22.22 mm to 28.57 mm on forehead and crown. Filaments on the head white, pale gray at the base; neck and body down pale gray, darker at the base. Pinfeathers just emerging on the crown.

Unfeathered Parts

Forehead and crown medium gray; top of neck greenish gray; skin over the eyes dark gray fading to pale gray around the eyes; lores and rictus pale orange-yellow. Back pale gray to green-gray, darker distally to deep gray around the cloacal region. Neck pale yellow-green ventrally, blending to pale yellow-gray on the breast; abdominal area gray-green, deep gray around cloacal region. Upper mandible greenish gray proximally, darker distally; culmen dark greenish gray to black distally; small ivory tip; line above cutting edge yellow-gray at commissural point to greenish gray distally; nostril arch pale greenish gray; egg tooth present. Lower mandible pinkish yellow blending to dark gray distally; small ivory tip; cutting edge pale gray. Mouth lining pale pink to pink. Iris pale gray-yellow, darker in some; eye-ring pale greenish gray. Top of tarsus medium gray-green, yellow-gray below; toes greenish gray above, yellowish gray below; nails pale gray.

Measurements

Body length 161.9 mm; wing 20.6 mm; bill 22.2 mm; tarsus 30.2 mm; middle toe 19.1 mm.

Age Seven Days

Plumage

Head, neck, and body covered with down; crown and nape with white down, pale gray at the base, longest (19.05 mm) on the crown; back covered with pale gray down; head, neck, wings, and back with emerging pinfeathers; breast, abdomen, and femoral pinfeathers emerging. All pinfeathers down-tipped, no rectrices appearing.

Unfeathered Parts

Skin of body dark gray-green; breast and abdomen yellow-green, cloacal region flesh color; skin varies in color intensity, some lighter and some darker but all nestlings in this age group have a greenish skin. Lores and rictus pale yellow to pale orange-yellow. Upper mandible greenish black; elongated area just above the cutting edge from the commissural point to one-half to two-thirds the length of the bill yellow; ivory tip on some bills barely indicated; egg tooth present. Lower mandible yellow proximally blending to greenish black distally; some individuals have very little black on the lower bill; small ivory tip. Mouth lining pale grayish pink to pink to bluish pink. Iris grayish yellow to deep yellow; eye-ring yellow to pale greenish gray. Tarsus yellowish green to grayish green above, varying to dark green on some young birds; tarsus yellow or orange-yellow to pale gray-yellow below; toes dark gray-green above, pale yellow below; nails pale gray.

Measurements

Body length 171.5 mm; wing 34.9 mm; bill 22.2 mm; tarsus 39.7 mm; middle toe 31.8 mm; longest primary pinfeather 7.9 mm; longest secondary pinfeather 11.1 mm; longest scapular pinfeather 19.1 mm.

Age Nine Days

Plumage

Head, neck, and body covered with down. Forehead and crown covered with white down, pale gray at the base, longest filaments vary from 19.05 mm to 31.75 mm on forehead and crown. Neck and body down pale gray, darker at the base; back heavily down-covered. Pinfeathers emerging on dorsal and ventral tracts, and are tipped with down; all quills down-tipped, scapular quills feather-tipped; no tail quills.

Unfeathered Parts

Body skin varies in color, lighter in some, darker in others; but all nestlings near this age have greenish skin. Head and body grayish green, darker on the forehead and crown, blending to pale gray over the eyes; neck pale gray to pale grayish green dorsally, reddish ventrally, greenish in some individuals; orbital region grayish blue, blending to pale greenish yellow at the eye-ring; lores and rictus pale orange-yellow; breast and abdominal areas pale yellow-green; cloacal region flesh color. Upper mandible dark greenish gray proximally; culmen black distally; edges of nostril arch yellow; elongated area just above the cutting edge from the commissural point to one-half to two-thirds the length of the bill is yellow to pale gray proximally, dark greenish gray distally; small ivory tip on some bills barely indicated; egg tooth present. Lower mandible pale gray or yellow proximally blending to greenish black distally; some lower mandibles have very little black; cutting edge pale yellowish gray; small ivory tip. Mouth lining grayish pink to bluish pink. Iris grayish yellow to deep yellow; eye-ring yellow to pale greenish gray. Tarsus pale yellow-green to pale grayish green above, yellow or pale orange-yellow below; toes grayish green above, some darker, and pale yellow below; nails pale gray.

Measurements

Body length 222.3 mm; wing 38.1 mm; bill 27.0 mm; tarsus 44.5 mm; middle toe 34.9 mm; longest primary pinfeather 9.5 mm; longest secondary pinfeather 15.9 mm; longest scapular pinfeather 11.1 mm; emergence of scapular feathers from sheaths 6.4 mm.

Age Twelve Days

Plumage

White down on the forehead and crown, heaviest and longest on the crown; back covered with medium gray down. Pinfeathers emerging on all dorsal and ventral tracts. Primary, secondary, tail, and crown pinfeathers are down-tipped.

Unfeathered Parts

Skin of upper back deep gray-green, fading to greenish on the lower back; abdominal area yellow-green to greenish in cloacal region; some nestlings have deep gray-green over entire back surface, but the basic skin color is green, varying in intensity. Lores and rictus orange-yellow. Upper mandible greenish black proximally, blending to black distally; small ivory tip; edge of nostril arch pale orange-yellow; elongated area just above the cutting edge from the commissural point to one-half the length of the bill is yellow to pale yellow or pale orange-yellow proximally blending to greenish black distally; cutting edge yellow proximally to pale yellow distally; egg tooth present. Lower mandible yellow, blending to black distally; cutting edge yellow proximally to pale yellow distally; small ivory tip. Mouth lining pink to bluish pink. Iris deep yellow; eye-ring yellow. Tarsus pale yellow-green above; yellow to pale yellow below; toes pale yellow-green above, pale yellow to pale gray-yellow below; nails pale gray. Scales forming on tarsi and toes.

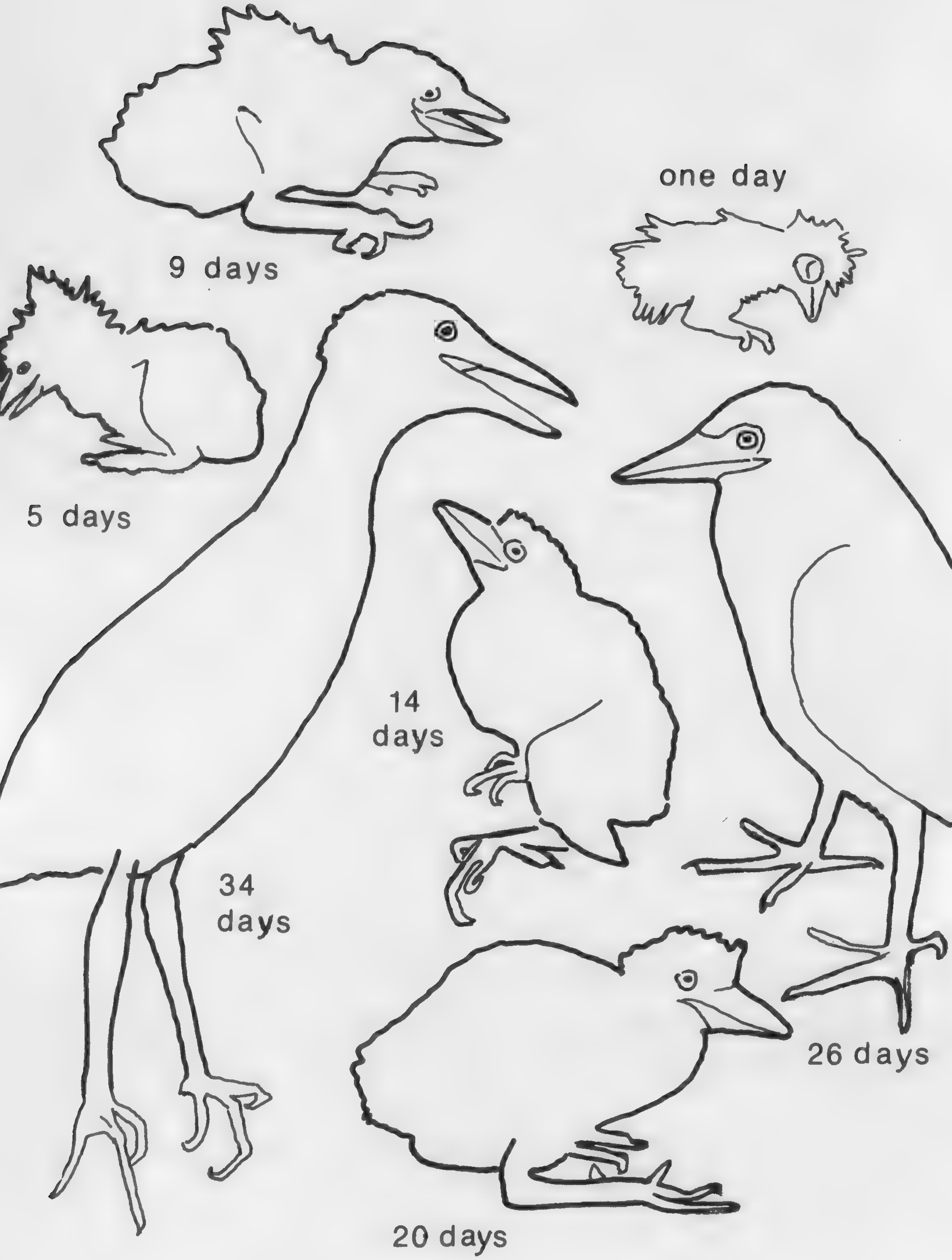
Measurements

Body length 228.6 mm; wing 44.5 mm; bill 28.6 mm; tarsus 50.8 mm; middle toe 39.7 mm; longest primary pinfeather 11.1 mm; longest secondary pinfeather 15.9 mm; longest scapular pinfeather 19.1 mm.

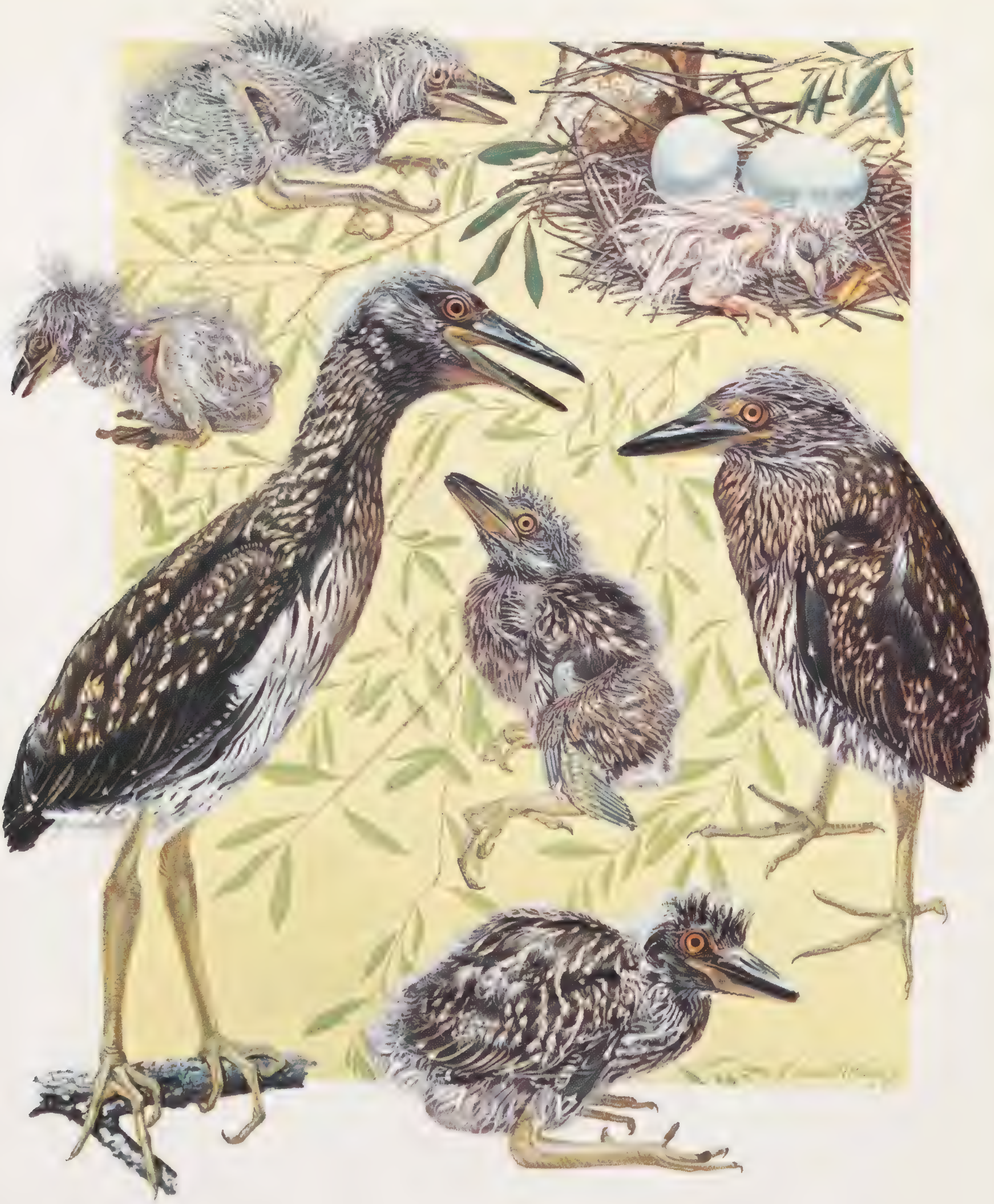
Age Fourteen Days

Plumage

White down on forehead and crown, longest (38.1 mm) on crown where down feathers have a dark base. Head, neck, and body covered with emerging down-tipped pinfeathers and others emerging from sheath. All wing feathers emerging from their sheaths. Emerging secondaries are deep gray, almost black; scapulars and wing coverts are deep brownish gray tipped with V-shaped pale buff spots; V-shaped spots on the coverts vary from off-white on the greater primary and secondary coverts to pale buff on the median and lesser coverts; on abdominal feathers, the outer vane is white, the inner vane black; lower abdominal feathers are white.



YELLOW-CROWNED NIGHT HERON



Unfeathered Parts

Exposed body skin dark gray-green dorsally, pale yellow-green ventrally; neck reddish or grayish ventrally; lores and rictus orange-yellow. Upper mandible dark greenish gray proximally to darker distally; small amber tip; nostril arch paler than culmen, edge of nostril arch pale yellow-gray; elongated area just above the cutting edge from the commissural point to one-half the length of the bill is pale gray proximally blending to greenish black distally; egg tooth present. Lower mandible pale yellow-gray proximally blending to greenish black distally; small pale amber tip. Mouth lining pink to bluish pink. Iris orange-yellow; eye-ring pale greenish gray to grayish yellow. Tarsus and toes pale grayish green above; tarsus orange-yellow below; toes pale yellow to orange-yellow below; nails pale horn with pinkish tint. Scales well formed on tarsi and toes.

Measurements

Body length 247.7 mm; wing 76.2 mm; tail 11.1 mm; bill 30.2 mm; tarsus 50.8 mm; middle toe 46.0 mm; length of emergence from sheath of fifth secondary 6.4 mm; emergence of longest scapular 19.1 mm; primaries just breaking through sheaths.

Age Fifteen Days

Plumage

Head, neck, and body covered with pinfeathers, some feathers emerging from sheaths. White down up to 19.05 mm attached to emerging juvenal feathers of the forehead and crown. Feathers of back have emerged; down on the back is medium gray. Scapulars emerging. Primary quills feather-tipped; secondary quill feathers emerging; wing coverts emerging; rectrices emerging, down-tipped; juvenal feathers emerging from their sheaths on the ventral tract of the neck, breast, and abdomen.

Unfeathered Parts

Body skin medium green; breast and abdomen yellow; cloacal region greenish; lores and rictus orange-yellow to yellow. Upper mandible greenish black; small ivory tip; egg tooth present; elongated area just above the cutting edge from the commissural point to one-half the length of the bill is pale yellow to yellow, blending to greenish black distally. Lower mandible yellow proximally blending to black distally; small ivory tip. Mouth lining pale grayish pink to bluish pink. Iris yellow to orange-yellow; eye-ring yellow. Tarsus light greenish yellow to yellowish green to grayish yellow-green above; tarsus and toes yellow below; nails pale gray; scales well formed on tarsi and toes.

Measurements

Body length 254.0 mm; wing 63.5 mm; tail 6.4 mm; bill 31.8 mm; tarsus 60.3 mm; middle toe 50.8 mm; longest primary pinfeather 30.2 mm; longest secondary pinfeather 25.4 mm; longest tail pinfeather 6.4 mm; longest scapular pinfeather 19.1 mm; primaries and rectrices just beginning to emerge from sheaths; length of emergence from sheath of fifth secondary 11.1 mm; emergence of longest scapular 12.7 mm.

Age Twenty Days

Plumage

Head, neck, and most of the body covered with juvenal feathers emerging from their sheaths; feathers of the back and rump tipped with down. White down on ends of juvenal feathers of forehead and crown; some wing and body feathers tipped with gray down. Primary feathers black with small white tips; secondary feathers black, no tipping; scapulars and feathers of upper back dark gray with brownish sheen, each feather tipped with elongated V-shaped buffy spots. Greater primary coverts black with brownish sheen, tipped with triangular spots; greater secondary coverts dark gray with brownish sheen, tipped with V-shaped white to buffy spots, and with pale buff edging on outer vane; median and lesser coverts dark gray with brownish sheen, tipped with V-shaped buffy spots, the outer vane edged with pale buff; marginal coverts dark gray with brownish sheen, tipped with small V-shaped buffy spots. Feathers of forehead black with reddish brown shaft; crown feathers black with white shaft. Emerging rectrices black; throat feathers white edged with pale buff; neck feathers white edged with dark gray; lower neck feathers more buffy, less white, and edged in dark gray; inner vane dark gray; some under-neck feathers near the breast and some central breast feathers have white outer vane; breast feathers dark buff edged in dark gray; upper abdomen pale gray edged in dark gray; lower abdominal feathers white, edged in dark gray merging to white under-tail coverts.

Unfeathered Parts

Back and rump dark gray-green; abdomen yellow-green; lores and rictus orange-yellow to yellow. Upper mandible greenish black proximally blending to black distally; cutting edge pale gray to pale yellow-gray proximally, fading to deep gray distally; small ivory tip. Lower mandible pale yellow to pale grayish yellow proximally, blending to black distally; small ivory tip. Iris yellow to orange-yellow; eye-ring grayish yellow. Tarsus and toes pale greenish yellow to darker greenish yellow above; tarsi pale greenish yellow, grayish yellow, or pale orange-yellow below; toes pale grayish yellow to pale orange-yellow below; nails medium horn.

Measurements

Body length 292.1 mm; wing 200.0 mm; tail 25.4 mm; bill 36.5 mm; tarsus 66.7 mm; middle toe 60.3 mm; length of emergence from sheath of fifth primary 28.6 mm; emergence of fifth secondary 38.1 mm; emergence of longest rectrix 6.4 mm; emergence of longest scapular 47.6 mm.

Age Twenty-six Days

Plumage

Head, neck, wings, and body completely covered with juvenal feathers, only the lower abdominal and cloacal regions bare. White down remains attached to emerging juvenal feathers on emerging forehead and crown feathers; some down remains attached to wing and body feathers. Primaries and secondaries black with small white tips on primaries only; rectrices black. Wing and body feathers same as described for age twenty days.

Unfeathered Parts

Lores and rictus skin yellow or orange-yellow; cloacal region green. Upper mandible greenish black proximally to black distally; small ivory tip; cutting edge pale yellow proximally, blending to black distally. Lower mandible yellow proximally, blending to black distally; cutting edge pale yellow; small ivory tip. Iris yellow; eye-ring yellow. Mouth lining pale pink to bluish pink. Tarsus and toes pale greenish yellow above, pale yellow to greenish yellow below; nails medium horn.

Measurements

Body length 342.9 mm; wing 165.1 mm; tail 44.5 mm; bill 41.3 mm; tarsus 76.2 mm; middle toe 53.9 mm; length of emergence from sheath of fourth primary 53.9 mm; emergence of fifth secondary 47.6 mm; emergence of longest rectrix 11.1 mm.

Age Twenty-nine Days

Plumage

Head, neck, wings, and body completely feathered, lower abdominal and cloacal regions bare. Lanceolated dark gray crown feathers edged in black; white down attached to the tips of the forehead and crown feathers; scapular and back feathers brownish black tipped with elongated V-shaped buffy spots; some pale gray down remaining on the body feathers. Primaries and secondaries black, small white tips on primaries only; median primary coverts black with more elongated triangular white tips; marginal coverts black with white tips; greater secondary coverts have V-shaped buffy to white tips and outer vanes edged in pale buff; median and lesser secondary coverts tipped with elongated V-shaped pale buff spots and with outer vanes edged in pale buff; marginal coverts black-tipped with small V-shaped buffy spots. Rectrices black. Under-neck feathers off-white to buffy white, edged in deep gray. Breast and abdominal feathers white, edged in deep gray or black; under-tail coverts white.

Unfeathered Parts

Lores and rictus skin yellow to orange-yellow. Upper mandible greenish black proximally to black distally; cutting edge pale yellow; small ivory tip. Lower mandible deep yellow proximally, blending to black distally; cutting edge pale yellow; small ivory tip. Iris deep yellow; eye-ring greenish yellow. Mouth lining pale grayish pink to bluish pink. Tarsus and toes pale green to pale yellow-green above, yellow below; nails medium horn.

Measurements

Body length 393.7 mm; wing 177.8 mm; tail 47.6 mm; bill 44.5 mm; tarsus 82.5 mm; middle toe 60.3 mm; length of emergence from sheath of fifth primary 66.7 mm; emergence of fifth secondary 60.3 mm; emergence of longest rectrix 25.4 mm.

Age Thirty-Six Days

Plumage

Head, neck, wings, and body fully feathered, some white down remaining on the head and pale gray down on the body. Forehead feathers black with brown shafts; crown feathers black with white shafts; ventral neck feathers brownish black with elongated V-shaped buffy spots; scapular and back feathers brownish black with V-shaped buffy spots; primaries black with white tipping; secondaries black; greater primary coverts black with small white triangular tips; greater secondary coverts brownish black with small V-shaped white tips, and with outer vanes edged in pale buff; median, lesser, and marginal coverts brownish black with V-shaped white tips; breast feathers buff, edged in deep gray; abdominal feathers are an intermixture of pale gray feathers with broad dark gray edging, and white feathers with outer vanes tipped in dark gray; toward the tail abdominal feathers are white with pale gray edging; under-tail coverts are white to off-white.

Unfeathered Parts

Lores and rictus orange-yellow, greenish yellow in some. Upper mandible black with greenish sheen; cutting edge orange-yellow to greenish yellow, darker distally; small amber tip. Lower mandible greenish yellow proximally, blending to black distally. Iris orange-yellow; eye-ring orange-yellow, greenish yellow in some. Mouth lining pink to bluish pink. Tarsus pale greenish yellow above; toes pale greenish yellow above, grayish yellow in some; toes pale orange-yellow below; nails medium horn.

Measurements

Body length 425.5 mm; wing 215.9 mm; tail 69.9 mm; bill 50.8 mm; tarsus 107.9 mm; middle toe 65.1 mm; length of emergence from sheath of fifth primary 120.6 mm; emergence of fifth secondary 101.6 mm; emergence of longest rectrix 66.7 mm.

SNOWY EGRET

Eggs

Females usually lay three to five eggs, elliptical in shape, and pale bluish green in color.

Age One Day

Plumage

Head, neck, and body covered with white down, longest (19.05 mm) on head.

Unfeathered Parts

Skin of forehead and crown dark pinkish gray; medium to dark blue around the eyes; top of neck grayish green; crown grayish green in some; back skin varies from pale, medium, or dark gray to dark greenish gray; wings pale grayish to pinkish; neck gray ventrally, greenish yellow in some; abdomen gray to greenish gray; gular pouch pinkish yellow to pinkish. Upper mandible pale pinkish gray, culmen darker distally; tip black; egg tooth present. Lower mandible pale to dark pinkish gray distally; tip black. The culmen, sides, and nostril arch of some chicks vary from pale yellow to pinkish yellow; both mandibles remain yellowish throughout the nestling and fledgling periods. Other day-old nestlings have a dark gray "saddle" beginning at the base of the upper mandible and extending to the proximal end of the nostril arch; lower mandible pinkish gray at hatching. Both mandibles turn completely black, except for the gray "saddle" over the culmen, at about age six to seven days and remain black through fledging. The "saddle" is not well defined on the upper bill of some nestlings and an occasional bird has an all black bill. Mouth lining pale pink. Iris pale gray to buffy gray; eye-ring gray. Tarsus pinkish gray to gray-green above, pale gray below; toes reddish pink, pinkish gray, or greenish gray above, pale gray below; nails ivory. The Snowy Egret chick can not be confused with any other "white" heron nestling—Common Egret, Cattle Egret, and Little Blue Heron. From age one day to fledging, the tarsi of the Snowy Egret are always darker than the toes.

Measurements

Body length 98.4 mm; wing 15.1 mm; bill 11.9 mm; tarsus 16.6 mm; middle toe 15.1 mm.

Age Four Days

Plumage

Head, neck, wings, and body covered with white down.

Unfeathered Parts

Skin of head and neck grayish green, some more pinkish; blue skin around the eyes; body and wings dark grayish green, some nestlings bluish green; neck greenish yellow ventrally; abdomen greenish gray; gular pouch pinkish.

At the age of three to four days, nestlings acquire a "dark" or "light" bill. Birds keep these distinct colorations through the nestling period. Dark bills gradually darken to black at six to seven days, except for a pinkish gray "saddle" area extending from the nostril arch over the culmen; the saddle usually turns black at about 20 days.

The dark- or black-billed birds have a dark gray upper mandible; culmen pinkish gray, darker distally, tip black; nostril arch pinkish gray to gray; egg tooth present. Lower mandible pinkish gray, darker distally ; tip black. Lower mandible turns black at six to seven days.

The light- or yellow-billed nestlings have a grayish yellow to yellow upper mandible; culmen pinkish yellow to pale grayish yellow, darker distally; tip black; egg tooth present. Lower mandible pinkish gray to yellowish gray, darker distally; tip black. Mouth lining pale pink. Iris pale gray to buffy gray; eye-ring gray on dark-billed young; grayish yellow on light-billed young. Tarsus pale or dark grayish green above, pale gray below; toes pink, pale pinkish gray, or pale grayish green above, pale gray below; nails ivory with darker tips.

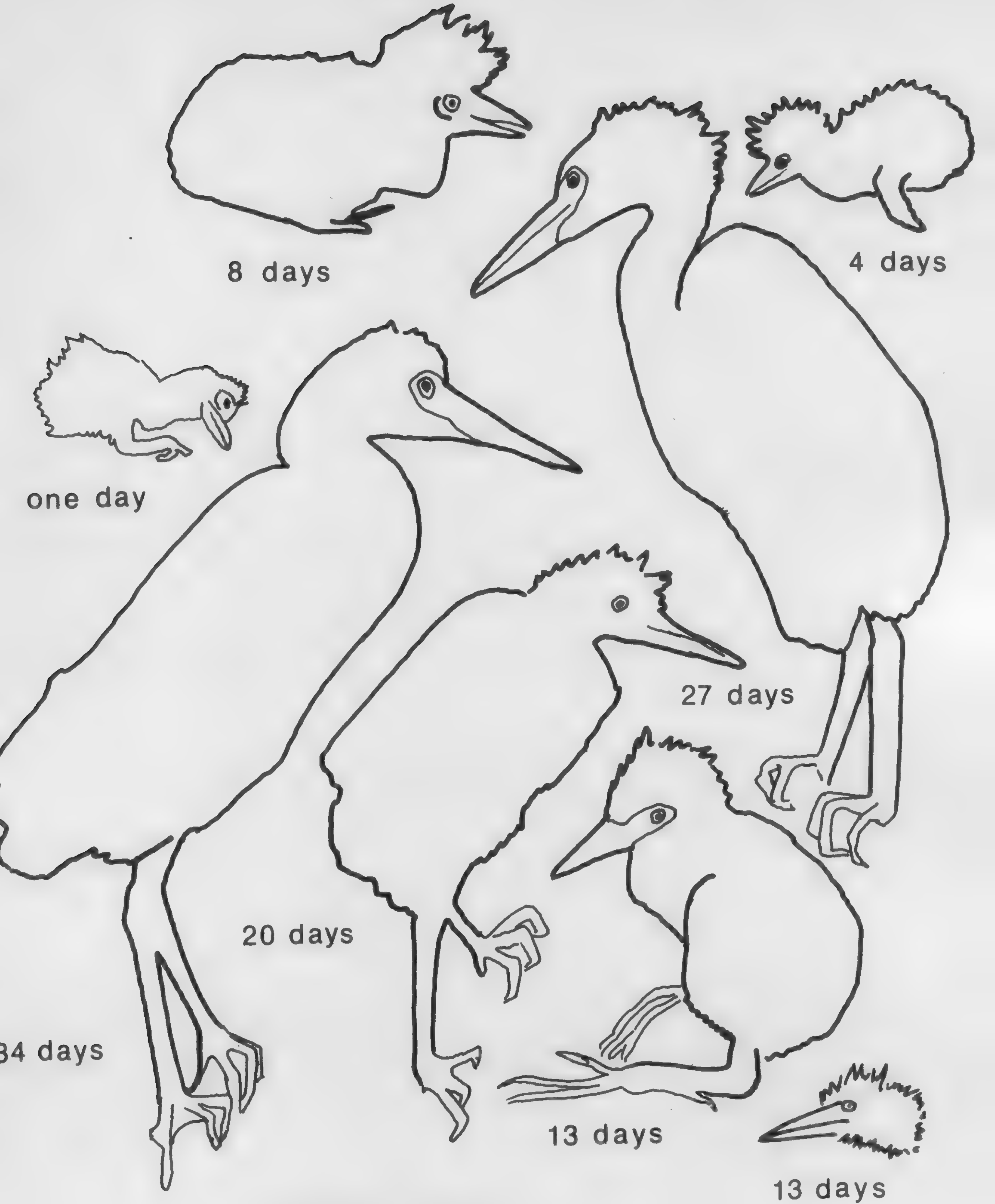
Measurements

Body length 139.7 mm; wing 22.2 mm; bill 15.9 mm; tarsus 25.4 mm; middle toe 20.1 mm.

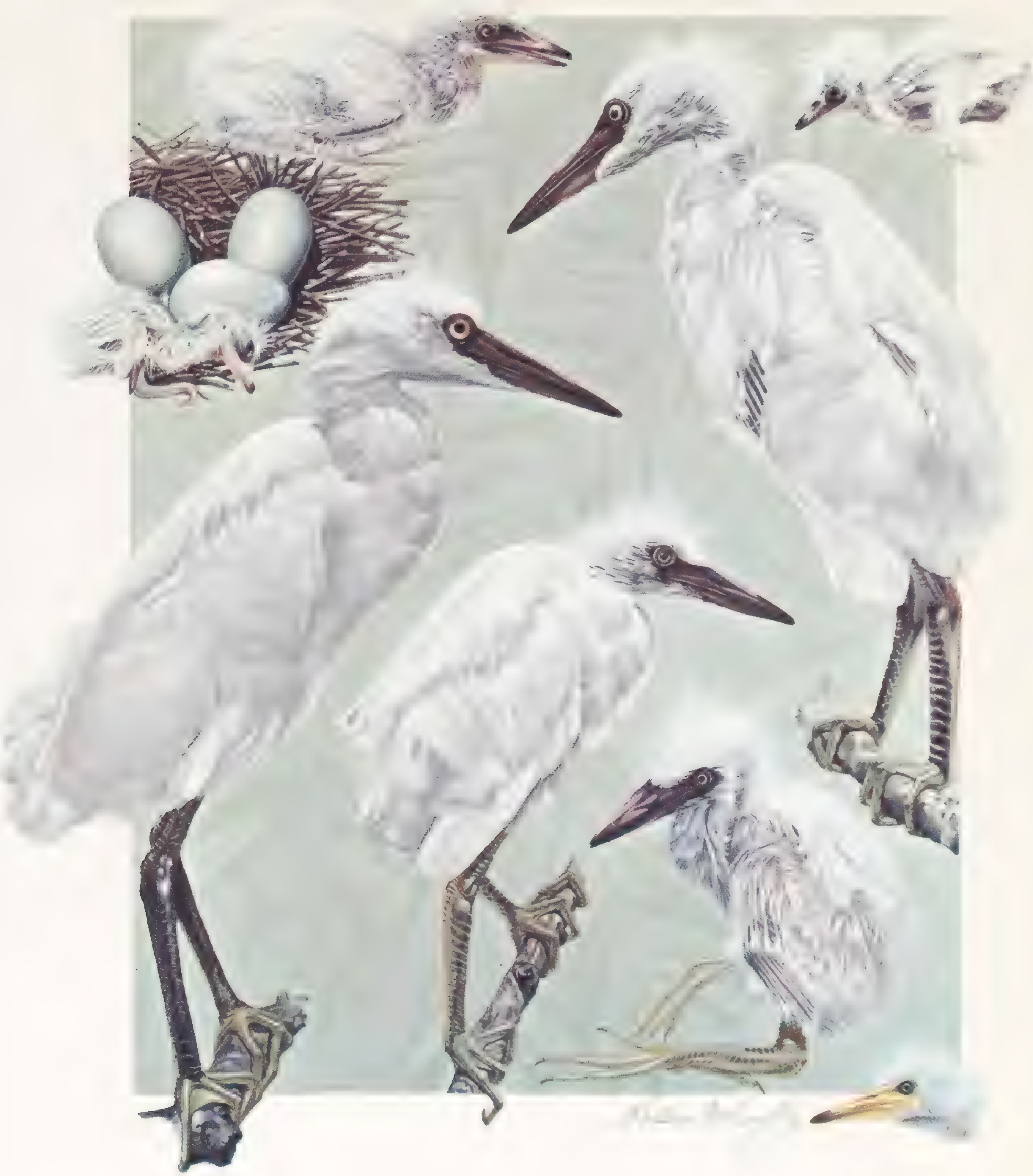
Age Eight Days

Plumage

Pinfeathers emerging on all feather tracts (dorsal and ventral). White down covering head, neck, wings, and body.



SNOWY EGRET



Unfeathered Parts

Skin of head, neck, and back grayish green; skin around the eyes grayish green, some individuals darker; gular pouch pinkish gray; neck, breast, and abdomen yellowish green.

Black-billed forms with deep gray to black upper mandible; tip black; egg tooth present. Lower mandible deep gray to black; tip black.

Yellow-billed young with yellow upper mandible, some birds with orange-yellow culmen and greenish yellow nostril arch; tip black; egg tooth present. Lower mandible yellow, blending to dark gray distally; tip ivory. Mouth lining pale pink to pink. Iris pale gray; eye-ring black on black-billed young; eye-ring yellow on yellow-billed young. Tarsus and toes grayish green to pale green above (some toes pale yellow-green); tarsus pale grayish yellow below; toes pale gray to pale grayish green below; nails pale horn.

Measurements

Body length 196.9 mm; wing 34.9 mm; bill 25.4 mm; tarsus 36.5 mm; middle toe 36.5 mm; length of longest primary pinfeather 9.5 mm; longest secondary pinfeather 11.1 mm; longest scapular pinfeather 12.7 mm.

Age Thirteen Days

Plumage

Juvenal feathers emerging on all feather tracts; rectrices just emerging; scapular, back, and abdominal feathers emerging; primaries, secondaries, and greater wing coverts emerging. Head and body covered with white down, longest (25.4 mm) on forehead and crown.

Unfeathered Parts

Skin of body gray-green dorsally; abdominal skin yellow-green; yellow-billed birds with greenish yellow lores and yellow rictus; black-billed birds with black lores and rictus.

Black-billed nestlings with black upper mandible; culmen and nostril arch gray; tomium pale gray; egg tooth present. Lower mandible black.

Yellow-billed nestlings with upper mandible yellow to grayish yellow; culmen reddish yellow; nostril arch greenish yellow; tomium yellow; egg tooth present. Lower mandible yellow blending to greenish yellow distally; tip black. Mouth lining pink. Iris off-white to pale gray; black-billed nestlings with black eye-ring; yellow-billed nestlings with greenish yellow eye-ring. Tarsus gray-green above, toes paler; tarsus and toes greenish yellow below; nails medium horn. Tarsi of yellow-billed nestlings are paler grayish green or yellowish green. At approximately ten days of age, the horny imbricated scales of the tarsi of the black-billed and yellow-billed young begin to darken (grayish green). At the age of thirteen days, the tarsi are definitely darker than the toes; the contrast is less in yellow-billed young.

Measurements

Body length 250.8 mm; wing 88.9 mm; bill 33.3 mm; tarsus 50.8 mm; middle toe 50.8 mm; length of emergence of fifth primary from sheath 4.8 mm; emergence of longest scapular 25.4 mm; rectrices and secondaries just beginning to emerge from sheaths.

Age Eighteen Days

Plumage

White juvenal feathers emerging on head and neck, white down present on forehead, crown, and neck; white juvenal feathers cover body, wings, and tail, some white down remaining on the back.

Unfeathered Parts

Black-billed birds with black lores and rictus; yellow-billed birds with yellow to greenish yellow lores and rictus.

Black-billed nestlings with black upper mandible; culmen pinkish gray, darker distally; tomium black; tip black. Lower mandible black; tip black.

Yellow-billed nestlings with yellow upper mandible, blending to black tip; tomium gray. Lower mandible grayish yellow, blending to black tip. Mouth lining pink. Iris pale grayish white; black-billed young with black eye-ring; greenish yellow eye-ring in yellow-billed nestlings. Tarsus gray-green above and below in black-billed forms; toes grayish green above, pale greenish below; nails pale horn with light tip; tarsi of yellow-billed young are paler.

Measurements

Body length 317.5 mm; wing 107.9 mm; tail 22.2 mm; bill 38.1 mm; tarsus 60.3 mm; middle toe 57.2 mm; length of emergence of third primary from sheath 19.1 mm; emergence of fifth secondary 15.9 mm; emergence of longest rectrix 9.5 mm.

Age Twenty-One Days

Plumage

White juvenal feathers emerging on head and neck, white down still present on head and upper neck; body, wings, and tail covered with white juvenal feathers; some down remaining on the body.

Unfeathered Parts

Black-billed birds with black lores and rictus; yellow-billed birds with greenish yellow lores and rictus.

Black-billed nestlings with black upper mandible; culmen pinkish gray; tip black. Lower mandible black.

Yellow-billed birds with yellow upper mandible, blending to a black tip; tomium pale gray. Lower mandible grayish yellow, blending to a black tip. Mouth lining pink, some reddish pink. Iris grayish white, some greenish white; eye-ring black in black-billed forms, greenish yellow in yellow-billed young. Tarsus gray-green above; scales dark gray, darker near the toes; heel orange-yellow to greenish yellow; tarsus pale grayish green below; toes usually grayish green above, yellowish green in some; toes pale yellowish green below; nails medium horn; tarsi and toes similarly colored in yellow-billed and black-billed young; some are paler in yellow-billed forms.

Measurements

Body length 330.2 mm; wing 120.7 mm; tail 31.8 mm; bill 50.1 mm; tarsus 60.3 mm; middle toe 57.2 mm; length of emergence of second primary from sheath 44.5 mm; emergence of second secondary 41.3 mm; emergence of longest rectrix 27.0 mm.

Age Twenty-seven Days

Plumage

Head, neck, wings, and body covered with white juvenal feathers; white down still on the crown; some white down remaining on the body.

Unfeathered Parts

Black-billed birds with black lores and rictus; yellow-billed birds with greenish yellow to yellow lores and rictus.

Black-billed nestlings with black upper mandible; tomium pale gray; tip black. Lower mandible black; tomium pale gray. Some nestlings still have a yellowish or pinkish gray saddle over the culmen and some yellow streaking on the lower mandible.

Yellow-billed nestlings with yellow upper mandible; tomium pale gray; tip black. Lower mandible grayish yellow, blending to a black tip; tomium pale gray. Mouth lining pink. Iris greenish white to off-white; black-billed young with black eye-ring; yellow-billed forms have greenish yellow eye-ring. Tarsus yellowish green above; imbricated scales dark gray, darker near the toes, some scales very dark; heel orange-yellow; tarsus grayish green below; toes yellowish green above, paler below; nails dark horn with light tips.

Measurements

Body length 361.8 mm; wing 165.1 mm; tail 31.8 mm; bill 54.0 mm; tarsus 63.5 mm; middle toe 54.0 mm; length of emergence of fifth primary from sheath 88.9 mm; emergence of fifth secondary 69.8 mm; emergence of longest rectrix 57.2 mm.

Age Thirty-four Days

Plumage

Head, neck, wings, and body fully feathered (white); some white down still attached to forehead and crown; very little down on body feathers.

Unfeathered Parts

Black-billed birds with black lores and rictus; yellow-billed birds with yellow lores and rictus.

Black-billed nestlings with black upper and lower mandibles; pale saddle area has almost disappeared at this age.

Yellow-billed nestlings with yellow upper mandible; tomium gray; tip black. Lower mandible grayish yellow to yellow, blending to a black tip; tomium gray. Mouth lining pink. Iris off-white; eye-ring deep gray to black in black-billed forms, greenish yellow in yellow-billed young. Tarsus very deep gray blending to black at the toes; heel gray-green; tarsus gray-green below, paler near the toes; toes yellow-green above, pale yellow-green below; nails dark horn with pale tips. Tarsi and toes of the yellow-billed young are sometimes paler.

Measurements

Body length 406.4 mm; wing 196.8 mm; tail 57.2 mm; bill 69.8 mm; tarsus 79.4 mm; middle toe 57.2 mm; length of emergence of fifth primary from sheath 133.4 mm; emergence of fifth secondary 120.7 mm; emergence of longest rectrix 34.9 mm.

620 S.R. 67 NORTH, VINCENNES, INDIANA 47591

Solitary Vireo, *Vireo solitarius*. Drawing by Lawrence B. McQueen.

SOCIAL BEHAVIOR OF THE BOAT-BILLED HERON [1]

DOUGLAS W. MOCK

Photographs by the author
Drawings by Nancy McGowan

The enigmatic Boat-billed Heron *(Cochlearius cochlearius)* has received a variety of taxonomic treatments since its description in 1760 (Brisson, 1760). Traditionally, it has been given its own monotypic family, Cochleariidae (Hellmayr and Conover, 1948; Wetmore, 1960), but recent authors have placed it in the Ardeidae (Bock, 1956; Cracraft, 1967; Dickerman and Juarez, 1971; and Payne, in press). Within the family Ardeidae, *Cochlearius* is usually placed among the night herons *(Nycticorax* spp.) and has even been called ". . . a curious travesty of the black-crowned night heron" (Dickey and van Rossem, 1938). Conversely, Dickerman, *in* Dickerman and Juarez (1971) argued that its differences merit tribal status, Cochleariini.

The taxonomic decisions to date have dealt primarily with preserved specimens and those characters that can be studied in museums. The major distinctions found between *Cochlearius* and other herons lie in the cranial osteology (Figure 1) and the number of powder-down patches. Wetmore (1960) outlined 10 skull differences and alluded to corresponding muscular differences associated with the much greater width of the bill. Bock (1956) and Cracraft (1967) maintained that these characters should be viewed as a single adaptive unit serving a hypothetical specialized feeding strategy.

Considering only the post-cranial skeletons, Cracraft (1967) found *Cochlearius* to be more similar to *Nycticorax* than were several other genera of "accepted" night herons. The significance of the extra pair of powder-down patches (four instead of three) is likewise poorly understood; however, this character is not constant even within the rest of the Ardeidae (e.g., the tiger-herons have three or four pairs). Other characters receiving attention include adult plumage (Bock, 1956), natal plumage (Dickerman and Juarez, 1971; Juarez, 1967) egg color (Blake, 1956; Dickerman and Juarez, 1971; Haverschmidt, 1969); and egg-white proteins (Sibley and Ahlquist, 1972). None of these characters supports a separate family for *Cochlearius.*

Meanwhile, the behavior of the Boat-billed Heron has remained almost totally unknown. Rand (1966) described the Crest Raising display from a zoo photograph which was later sketched in the field by Gavino (Dickerman and Juarez, 1971). Carpenter (1971) made observations at the Bronx Zoo, but detailed behavioral descriptions of wild Boatbills are entirely lacking.

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[1] This paper is contribution number 176 of the Welder Wildlife Foundation.

Unlike the Boat-billed Heron, many other heron species have been the subjects of ethological study. Extensive descriptions of natural behavior exist for the Grey Heron, *Ardea cinerea* (Milstein *et al.,* 1970; Verwey, 1930); Great Blue Heron, *A. herodias* (Cottrille and Cottrille, 1958; Meyerriecks, 1960; Mock, 1972); Great Egret, *Casmerodius albus* (Wiese, 1975); Louisiana Heron, *Hydranassa tricolor* (Rodgers, 1974 and 1975); Cattle Egret, *Bubulcus ibis* (Blaker, 1969; Lancaster, 1970); and Green Heron, *Butorides virescens* (Meyerriecks, 1960). Unfortunately, the night herons have been largely ignored except for scant descriptions by Allen and Mangels (1940), Noble *et al.* (1938), Voisin (1970), and unpublished studies by Meyerriecks. It is the purpose of this paper to describe natural Boat-billed Heron behavior, to evaluate the behavioral characters from a taxonomic point of view, and to discuss some evolutionary aspects of this unusual species.

Resident *Cochlearius* populations inhabit the wet neotropics from northern Mexico (both coasts) through much of South America (Figure 2). At least five subspecies have been described (Dickerman, 1973).

Methods

During the summers of 1973 and 1974, I studied Boat-billed Herons in a colony near San Blas, Nayarit, Mexico (Lat. 21° 33' N, Long. 105° 17' W). There it nests in red mangrove, *Rhizophora mangle* (Figure 3), among seasonal lagoons that fill rapidly with brackish water at the beginning of the rainy season (Figure 4). The Boat-billed Heron times its nesting cycle with the flooding of these low areas (Dickerman and Juarez, 1971) with a predictability that makes it convenient for colony research. My studies were done in the lagoon at the intersection of Highway 54 and the side road to Playa Matanchen. Also nesting in the mangroves were Great Egrets, Snowy Egrets *(Egretta thula),* Louisiana Herons, Little Blue Herons *(Florida caerulea),* Green Herons, and Anhingas *(Anhinga anhinga).* But the Boatbills nested apart, occupying mangrove clumps at the edge of the mixed colony and beyond. Dickerman and Juarez (1971) have described the habitat and nesting biology of the Boat-billed Heron at San Blas.

I made observations from a fixed blind (1973) and a floating blind (1974) that accommodated the fluctuating water levels (Figure 5). I cut a few of the outer mangrove branches to permit visibility into the thicket, but the birds did not seem aware of my presence once I had entered my blind. Observations were usually made from distances of less than 30 feet. Notes were either written or dictated into a portable tape recorder. Still photographs, movies, and sound recordings were made of as many behavior patterns as possible. Typically, I made daily observations in the colony from 45 minutes before dawn until mid-morning (when social activity subsided) through the pre-egg portion of the breeding cycle. With the onset of sustained incubation, I switched my efforts to collecting and diet analysis.

Thirteen Boat-billed Herons were shot for stomach content analysis. For comparison, eight Yellow-crowned Night Herons were also collected and examined. Stomach and esophageal contents were identified by Sr. Enrique Lozano, marine biologist of the University of Mexico, who has been studying estuarine ecology in this area for two years.

Vegetation density was sampled in eight randomly chosen square quadrats (measuring five feet per side) in the breeding colony. In each quadrat, planes were imagined at one-foot-height intervals from zero to eight feet above peak water level. The total number of trunks, limbs, and prop roots that intersected each imaginary plane was recorded as was height of canopy foliage. The data of the eight sample quadrats were pooled to represent an estimate for vegetation density in the whole colony.

In the same part of the colony used for the vegetation measurements, I estimated display heights during 12 observation periods. Nest heights were measured for 40 nests in this same area.

Because the sexes of *Cochlearius* could not be easily distinguished in the field, statements of sex roles are based on the few pairs that I felt I could recognize, on continuous observations that included a copulation, and on observations of birds collected for stomach analysis. All sex-role statements must be considered tentative.

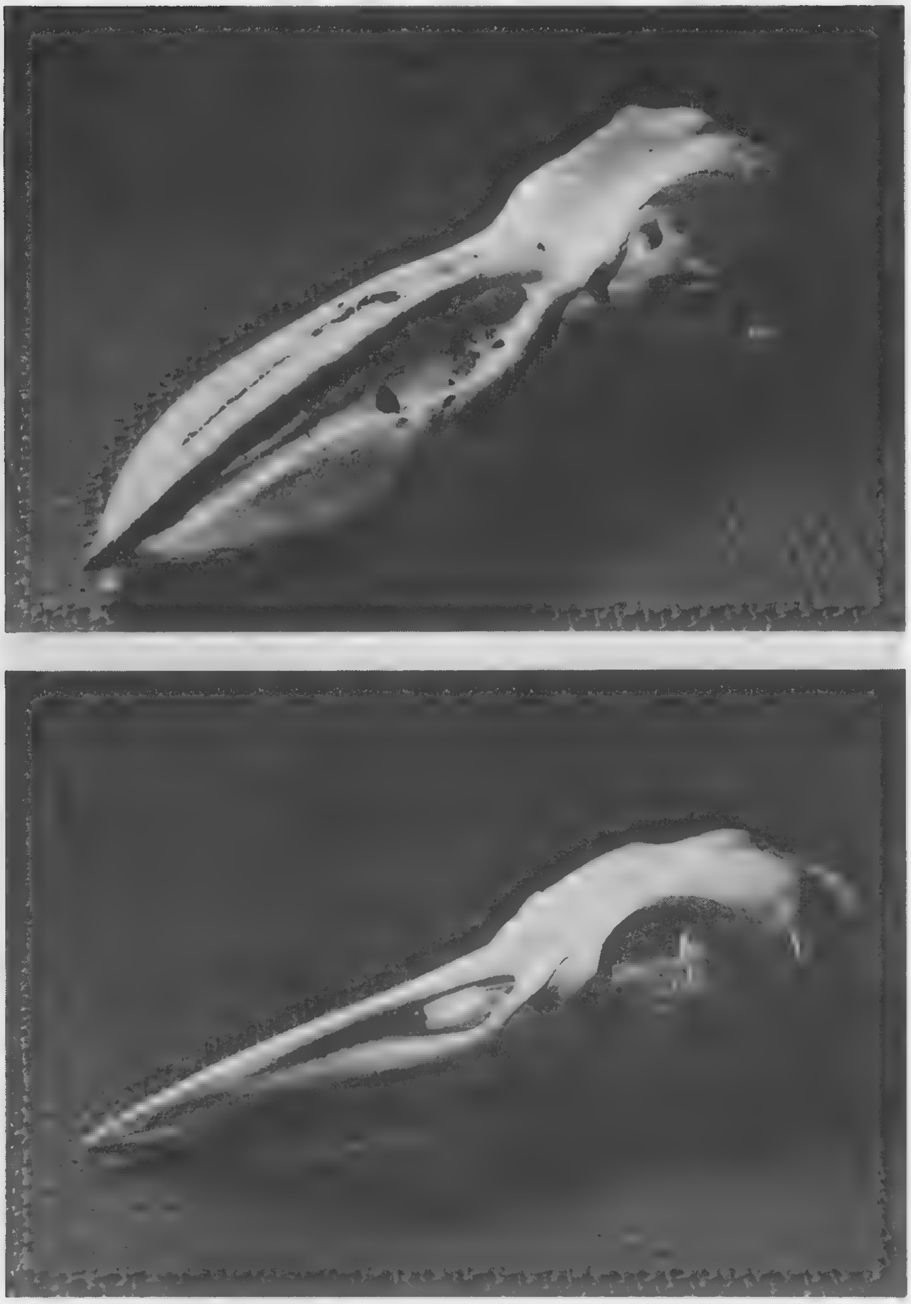


Figure 1. Skulls of *Cochlearius (above)* and *Nyctanassa,* contrasting bill shapes.

Locomotion

Flight

The flight of the Boatbill looks very similar to that of other herons. Wingbeats are unhurried and vary from deep (arc about 90°) to quite shallow (arc about 30°). Sometimes the deeper wingbeats produce a low frequency mechanical sound, but most flights are silent.

Hop-flight

To cross short openings in the mangrove thickets the Boatbill uses a long jump usually accompanied by one or two wingbeats. Distances covered by this method range from about one-half meter to five meters. Hop-flight locomotion is important in a habitat consisting of dense but non-continuous vegetation (Figure 6).

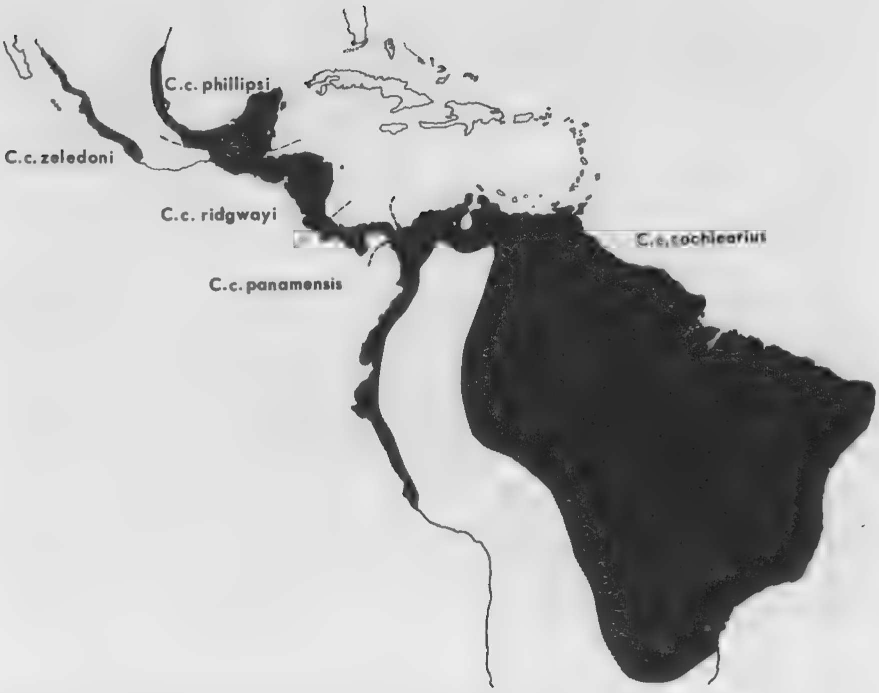


Figure 2: Range of *Cochlearius* with subspecies indicated.

Walking

Boatbills walk along mangrove limbs with a low hump-backed posture (horizontal to 45° angle) that enables them to pass under low branches. They have little trouble balancing on a linear trunk and only rarely use their wings for assistance. The head is usually kept within about 10 centimeters of the shoulders and often is held tight against them. With each step the toes are spread during the advance and are placed almost delicately on the limb. Sidestepping, without crossing the legs, is used only when a bird is moving short distances to one side (such as members of a mated pair shifting closer to one another).

Swimming

Like many herons that have been reported to swim (e.g., Hedeen, 1967), the Boatbill floats well and can move along the surface of the water. I have only seen this once, when a fighting heron was driven off its perch and fell into the water. The Boatbill kicked and flapped its wings until it reached the nearest prop root where it climbed out. Swimming may not be part of their voluntary repertoire.

Comfort Activities

Boatbills spend the greater part of the daylight hours resting and performing comfort activities. Indeed, the rising sun seems to trigger a change from social behavior to comfort behavior. On cloudy days, when the sun's warmth penetrates the mangrove thickets more gradually, this change is less dramatic; but on clear mornings it can be very abrupt and synchronous (within five minutes or less) for all the birds in the colony.

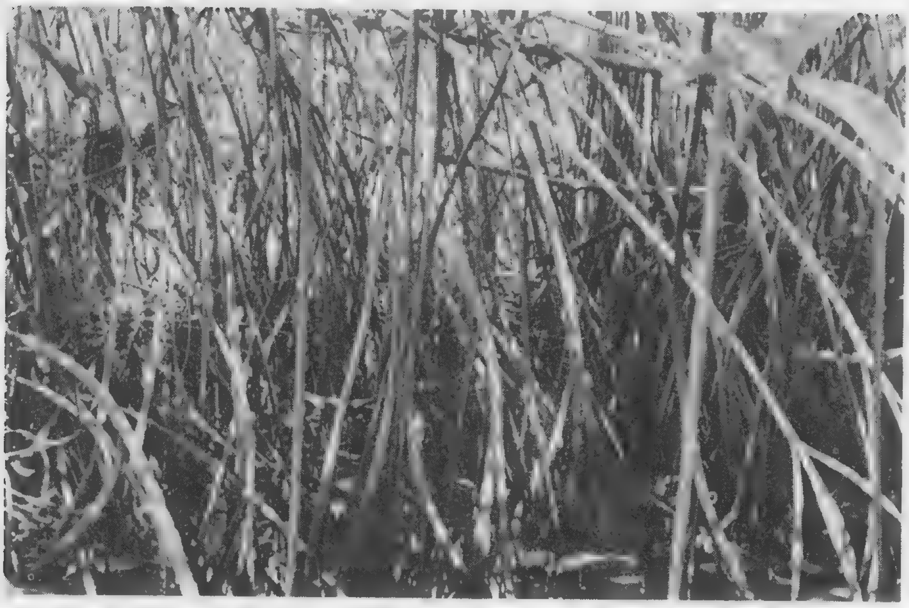


Figure 3. Boat-billed Heron nesting colony in red mangroves near San Blas, Mexico.

Resting postures.—A Boat-billed Heron stands typically with its head resting on its shoulders and its bill pointing forward and slightly below horizontal (Figure 7). The body axis is about 60° unless a strong wind forces the bird to balance in a more horizontal position. Boatbills usually stand on both feet, but one-legged standing is also fairly common. When alarmed the bird extends its head and neck upward and forward and raises its bill to slightly above horizontal. This "tall-alert" posture is often accompanied by erection of the occipital plumes.

Preening.—When preening, the Boatbill uses either the tip, or "nail," of the bill or the tomia midway back in the bill. It preens with both a stropping motion and a halting nibbling motion. Toes are also lifted and nibbled.

Oiling.—Oil is obtained by nibbling the uropygial gland at the base of the rump with the bill-tip. It is distributed to back, flanks, belly, and wings

Figure 4. Lagoon after flooding with 90 centimeters of brackish water.

with a stropping motion. Occasionally Boatbills rub their heads on the rump to dress the head feathers.

Powdering.—There are four pairs of powder-down patches on the body: breast, inguinal, flanks, and back. These yellowish talc-like feathers are pulled off in small amounts and held in the bill-tip. Then, normal preening motions distribute the crumbled powder-down to the body feathers. The head is powdered by tucking it into the breast patches and vigorously moving it back and forth. Head-scratching typically follows and may serve as a combing-out. Sometimes powder is distributed to the undersides of the wings by rubbing the powdered head against that area. The exact function of powder-down preening in herons is not known, although Wetmore (1920) suggested that it helps remove slime and may waterproof the plumage.

Scratching.—The pectinate claw on the middle toe is used as a scratcher and probably as a comb (especially with powder). The head is lowered halfway down the body and turned to the side as the foot is lifted under the wing for scratching. The crown, cheek, neck, and even the bill are frequently scratched during normal preening bouts.

Stretching.—Yawning ("jaw-stretch" of McKinney, 1965) is commonly seen during resting periods. The head and neck are lifted upward and forward and, as the gape widens, the lining of the throat may become momentarily everted over the bend in the neck. This brief eversion may rid the gular sac of mud and debris as described for Brown Pelicans, *Pelecanus occidentalis* (Laycock and Singletary, 1974). No other stretching movements were seen in the field, but Carpenter (1971) reported wing-and-leg stretch and both-wings stretch in captive Boatbills.

Shaking.—The body-shake (McKinney, 1965) begins with a loose alternate tossing of the two wings followed by extension and brief rotation of the neck. Occasionally the neck-shake portion is omitted.

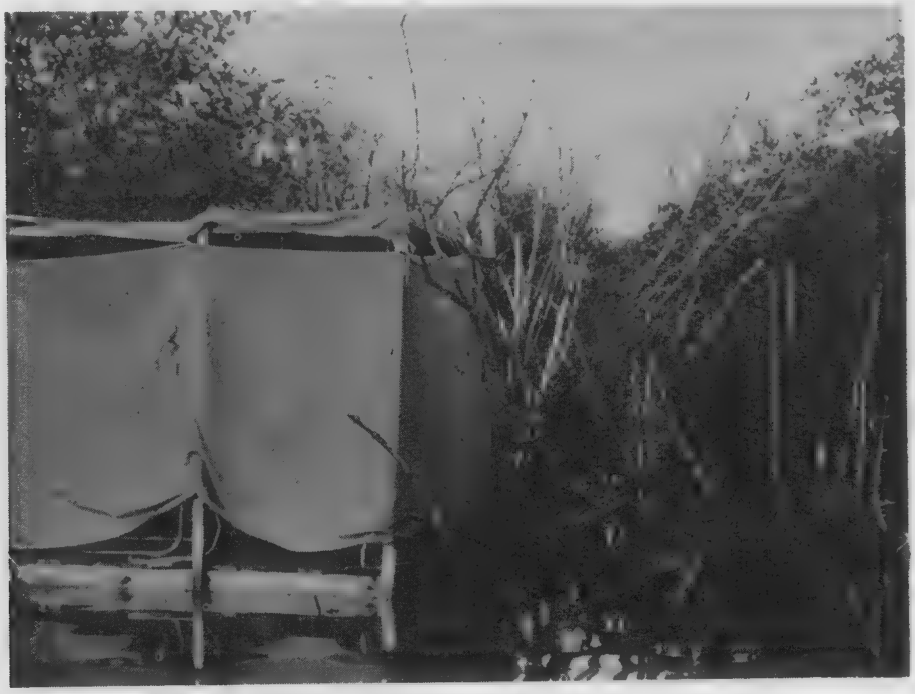


Figure 5. Floating blind used for colony observation.

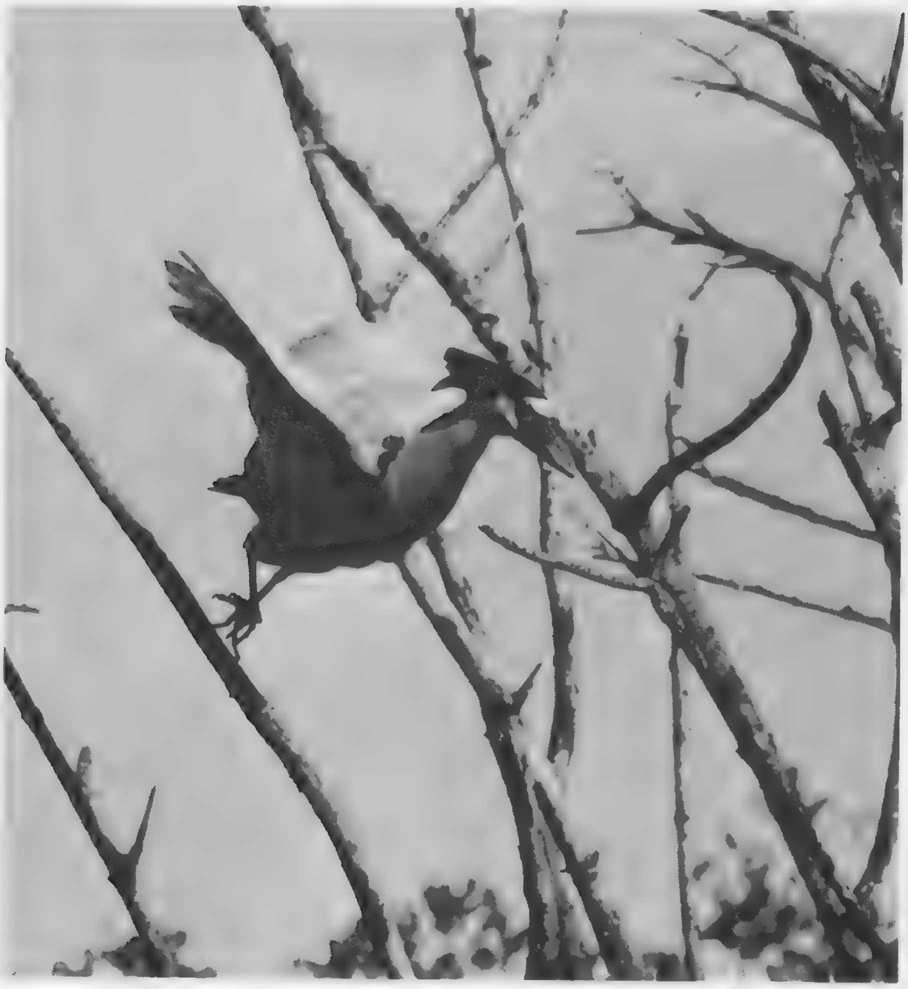


Figure 6. Hop-flight locomotion by a Boat-billed Heron.

Wing-flicking consists of sudden and very rapid movements of the wrists away from the body (about 2 cm) and back again. It occurs commonly during periods of preening or standing quietly, and also during rainstorms (probably repelling rainwater). Wing-flicking occurs in definite bouts. I observed one member of a pair give three to four wing-flicks per minute for twenty minutes while its mate did none; then they switched. This motor pattern may have additional signal function.

Head-shaking consists of one to four vigorous lateral twists of about 6-cm amplitude. The occipital crest flops from side to side during the shake.

Sleeping.—Perhaps because of its large bill, a Boatbill only rarely tucks its head backwards for sleep. Instead the head rests forward on the breast and the eyes are closed.

Care of the bill.—In addition to being scratched, the bill is also wiped and even washed. In wiping, the Boatbill slowly rubs the edge downward against a branch. The bill does not touch the limb during recovery; pressure is exerted only on the downstroke. After each stroke, the Boatbill changes sides and wipes the opposite edge. The bill is washed by dipping it vertically into the water, withdrawing it, and giving a head-shake to remove excess water.

Oral comfort movements.—Sometimes Boatbills rapidly (about four times per second) open and close their bills without making any sounds. This "mandibulating" seems to have no obvious signal features and probably is merely a comfort movement of unknown function. Although it resembles Bill-clappering, the rate is much slower, no audible sounds are produced, and no display recipient is present.

Boatbills also perform pumping motions with the tongue-hyoid apparatus that are visible to the observer (the flexible gular sac moves) and closely resembles tongue-movements found in other herons (pers. observ.).

Defecation.—In the colony, Boat-billed Herons make no attempt to avoid defecating into the water. This contrasts with the behavior reported for other herons on the feeding grounds (Brackbill, 1966; Recher and Recher, 1972). The bird merely stands, flexes its legs, and releases the feces.

Bathing.—I have never seen a Boatbill, or any other heron, bathe.

Social Behavior

When the seasonal rains flood the lagoons with brackish water, the Boat-billed Herons begin nesting in the lagoons' mangrove thickets (Dickerman and Juarez, 1971). By the date of my arrivals in early July, there were already adult birds spending the daylight hours roosting among the prop roots. Because the existing nests were mostly ignored, they probably represented the previous year's efforts. By mid-July the Boatbills began to defend territories and carry sticks to nest sites.

In contrast to the typical pattern found in other herons (e.g., Meyerriecks, 1960), single male Boatbills were never seen alone on territories performing long series of "courtship" displays. There were already a few pair-bonded birds when I arrived both seasons; additional pairs appeared in the thicket with the passage of time. There are at least five explanations for this apparent anomaly: (1) Boatbills may have permanent pair-bonds; (2) they may form

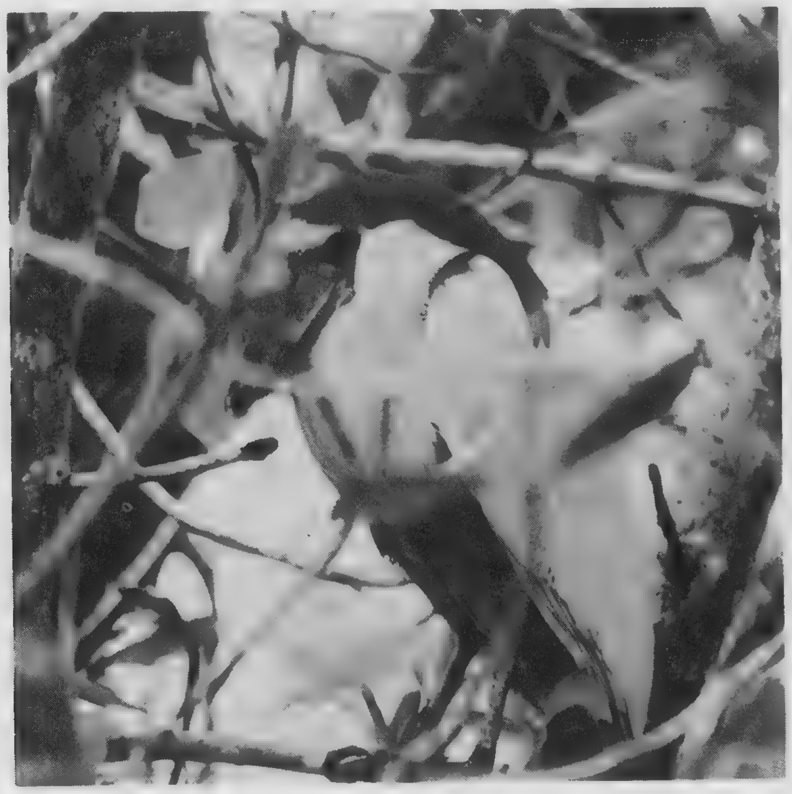


Figure 7. Normal resting posture of a Boat-billed Heron.

pairs away from the site of the nest; (3) they may form pairs at night; (4) they may form pairs well in advance of egg-laying; and (5) I may have failed to see pairing due to the reduced visibility in the nesting habitat.

Nevertheless, Boatbills do engage in a variety of social interactions in the vicinity of the nest-site. The displays presented here must be considered as a first attempt to describe and classify communication patterns for the species. I shall describe each display and its contexts and then discuss its possible functions and homologies. The definition of "display" is that of Moynihan (1955): ". . . those peculiarly standardized and often exaggerated performances, including all vocalizations and many movements and postures, which have become specialized and modified as social signals or releasers."

Single-bird Displays

This is a heterogeneous assemblage of social patterns that can be performed by an individual without the presence of a conspecific.

Crest Raising

The broad lanceolate plumes of the crown are erected and may be spread in a fan-shaped pattern. The blackness of the plumes contrasts strikingly with the white forehead. The degree of erection is highly variable, ranging from the slightest ruffling to 90° and more if a breeze pushes the feathers up from behind (Figure 8; see also Rand, 1966 and Dickerman and Juarez, 1971). The display may be extremely brief, the crest rising and falling in less than one second of nonstop motion, or it can be held for several seconds. Frequently the Boatbill also extends its neck up and forward with a slight arch while Crest Raising. Crest Raising is both a display in its own right (that is, performed by itself), and a component of various other displays including Tall Rocking, Single Clap, Pop, An-snap, Supplanting, and Bill-clappering.

By itself, Crest Raising occurs primarily in contexts of disturbance. Any kind of sudden movement or noise may elicit its performance. For example, I observed one individual Crest Raising in response to a Red-winged Blackbird *(Agelaius phoenicius)* that flew through the mangroves 10 feet from the heron. More typically, however, a heron performs in response to the arrival or approach of conspecifics, including the mate.

Many, if not all, other herons use Crest Raising both as a display and as an element of other displays. It has already been described for the Grey Heron (Verwey, 1930); Great Blue Heron, Snowy Egret, Reddish Egret *(Dichromonassa rufescens),* and Green Heron (Meyerriecks, 1960); Black-crowned Night Heron *(Nycticorax nycticorax)* (Noble *et al.,* 1938; Allen and Mangels, 1940); Cattle Egret (Blaker, 1969); Great Egret (Wiese, in press); and Louisiana Heron (Rodgers, 1974).

Scapular Erection

Although the scapular plumes are infrequently erected alone, this erection is typically a component of more complex signals. The relative lack of importance of the Scapular Erection as a signal is affirmed by the unspecialized structure of these feathers compared with the scapular plumes of many other herons. In *Cochlearius* they are scarcely longer than the flank contours and possess broad vanes. The Scapular Erection, too, has been

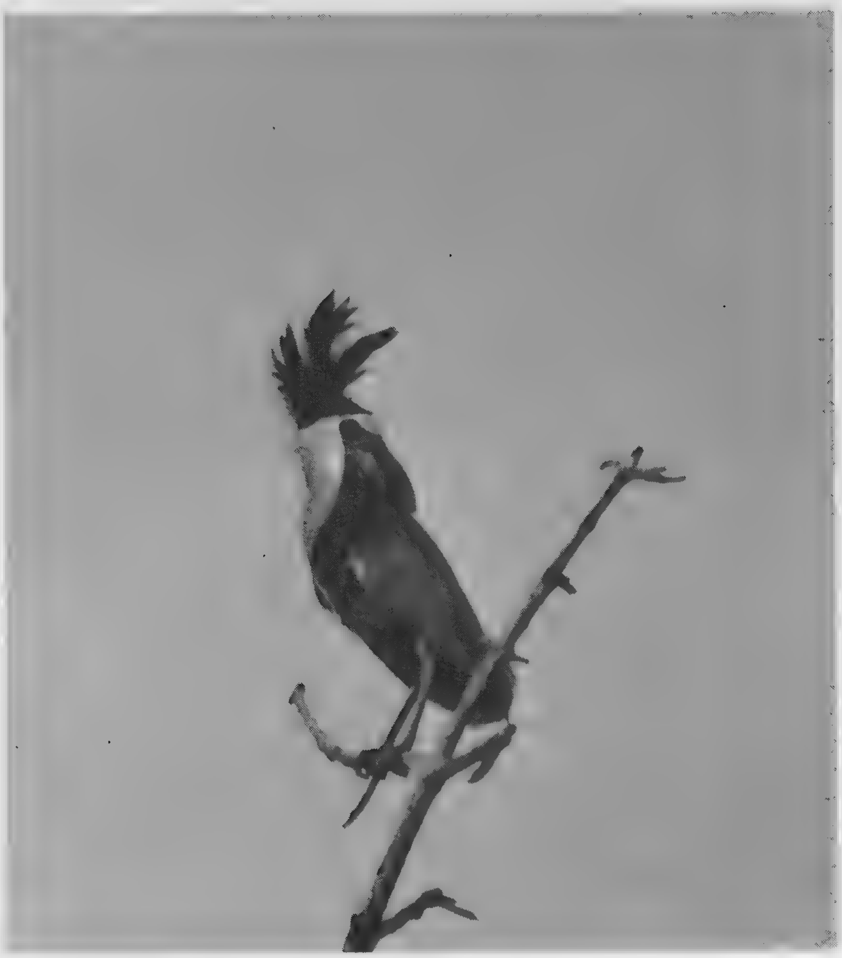


Figure 8. Crest Raising with breeze pushing plumes forward.

reported in many heron species (e.g., Meyerriecks, 1960) and other birds as well (e.g., Morris, 1956).

Tall Rocking

The displaying Boatbill extends its neck up and forward, raises its crest, usually erects all neck feathers, and rocks gently from side to side (Figure 9). The rocking motions are performed quite slowly, about one full cycle per second, and typically describe an arc of about 30° to each side. On two occasions Boatbills were seen making extremely wide-amplitude arcs; both performances were immediately followed by all-out attacks. Often there is a gradual bowing of the neck while rocking, which seems to render the erected crest more conspicuous. This bow, which involves a slight flexion of the legs at the heel, is not usually deep, although a horizontal or slightly sub-horizontal neck position may be assumed (Figure 9). Tall Rocking is performed by both sexes and is even used in "restrained fights" between mates.

Tall Rocking generally occurs in mildly to strongly aggressive situations (pre-threat to pre-fight) between strangers, neighbors, or mates. Usually, if the receiver of the signal does not move away, another display, such as Ansnap, and hostile approach follow. Sometimes Tall Rocking seems to be performed in response to a sudden increase in the general noise and activity level of neighbors rather than to a specific individual.

Thus, Tall Rocking probably functions as a mild threat that either can be escalated or abandoned. In addition, the elevation of the head affords the Boatbill a clearer view in the dense vegetation, an effect surely enhanced

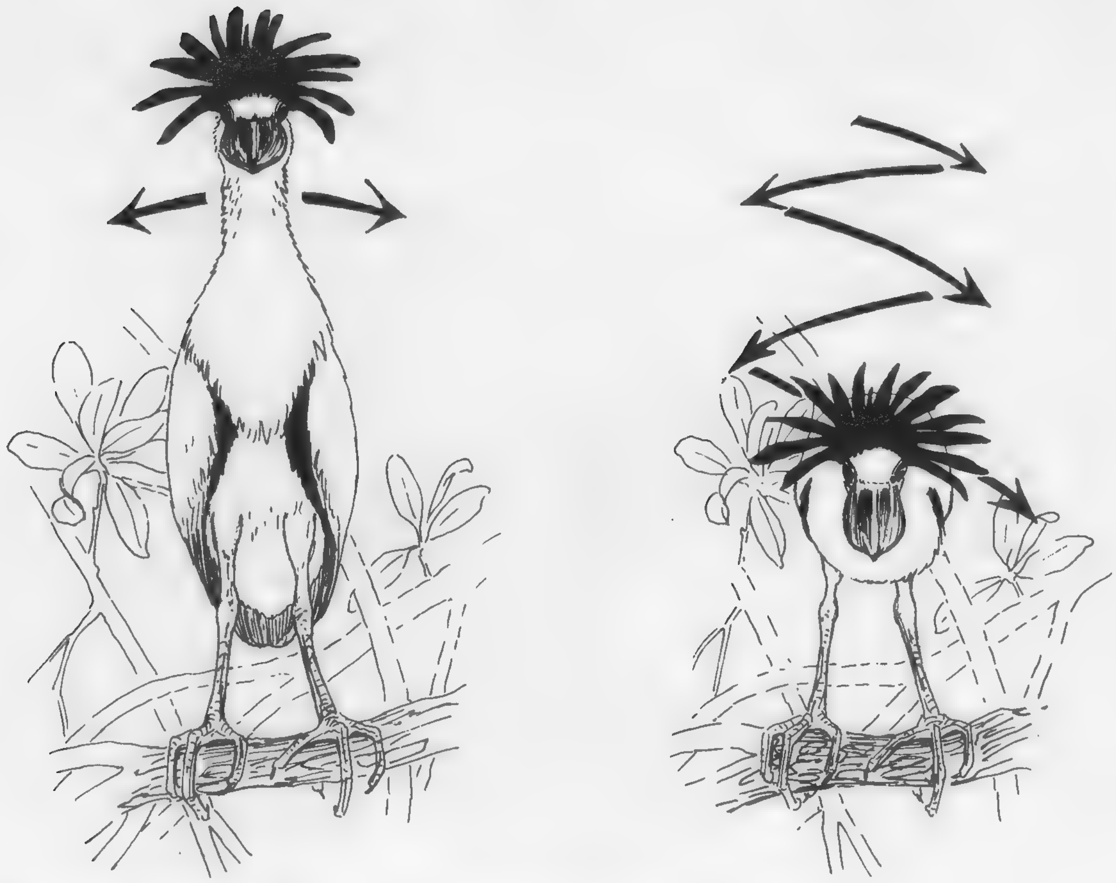


Figure 9. Tall Rocking in both its erect and bowing forms.

by the lateral movements. It seems plausible that this display was ritualized from a tall alert posture in which the bird was trying to peer around obstacles to see its opponent more clearly.

There are no described displays in other heron species that closely resemble Tall Rocking. The overall appearance of the Arched Neck in *Ardea* (Milstein *et al.,* 1970; same as Aggressive Upright of Meyerriecks, 1960) is reminiscent of the initial posture and contexts but lacks the motions of Tall Rocking. Tall Rocking is probably the display described by Rand (1966) but incorrectly assumed to be sexual in function.

Twig-shake

Sometimes, while engaged in a social interaction such as Long Chants or mutual Bill-clappering, the Boatbill turns to a nearby branch, seizes it, and shakes it for one to three seconds. The shaking motion is usually side-to-side and small in amplitude (less than 15 cm) but it can become quite violent; smaller branches may be waved as wildly as their springiness will permit. Twig-shakes involve living mangrove branches, parts of already built nests, or sticks floating in the water.

The Twig-shake is probably a ritualized form of normal stick-collecting movements. An alternative interpretation might be that it is a ritualized redirected attack; but the motor pattern of the Twig-shake resembles nesting movements far more than attack-stabs. Its claim to display status is supported by three lines of evidence: (1) the typically social context, (2) the frequent unsuitability of the vegetation involved (which can be far too thick for the bird to possibly break off), and (3) the very similar displays found in other

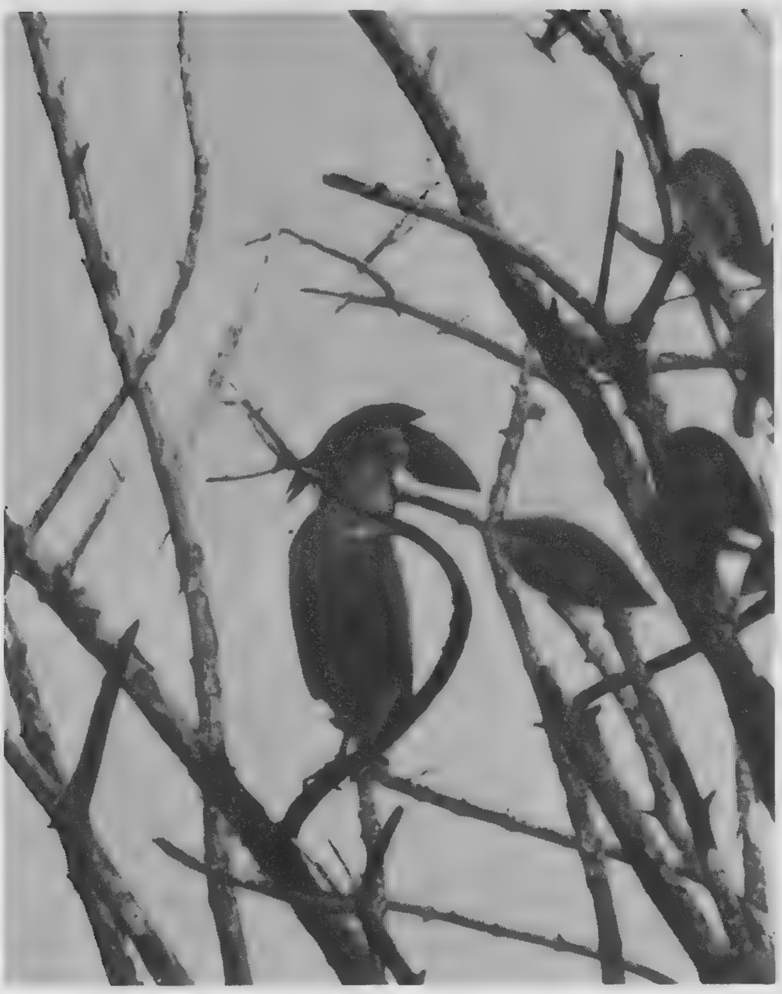


Figure 10. Short Chant. Note the expansion of the flexible gular sac.

herons, including the Great Blue Heron and Great Egret (pers. observ.) where Twig-shakes are both more stereotyped and more common.

Short Chant

This vocal display consists of a series of discrete, but similar, notes whose tone may be represented as "an" (a sound more accurately represented with the International Phonetic Alphabet: "ae n" or the French pronunciation of "ain"). Sometimes the notes change to slightly different tones, producing sound patterns like *oh-oh-ah-an-an* that rarely exceed 10 syllables. Pitch remains essentially even throughout the call. The call is not associated with any particular posture although the neck is usually partially extended as in the Tall Alert position (Figure 10).

The Short Chant is commonly performed in two contexts: when a Boat-bill walks around in the colony and when it perceives a mild danger stimulus, such as a human wading some distance away.

I suspect that the Short Chant alerts conspecifics to potential danger in the colony, thus providing the chanting bird with "more eyes" to watch for danger. It also serves as a contact call, announcing the bird's presence and movements through its territory.

Ascent Call

This is comprised of Short Chants whose pitch and volume suddenly rise as the "an" notes become more nasal in tone. This seems to happen at

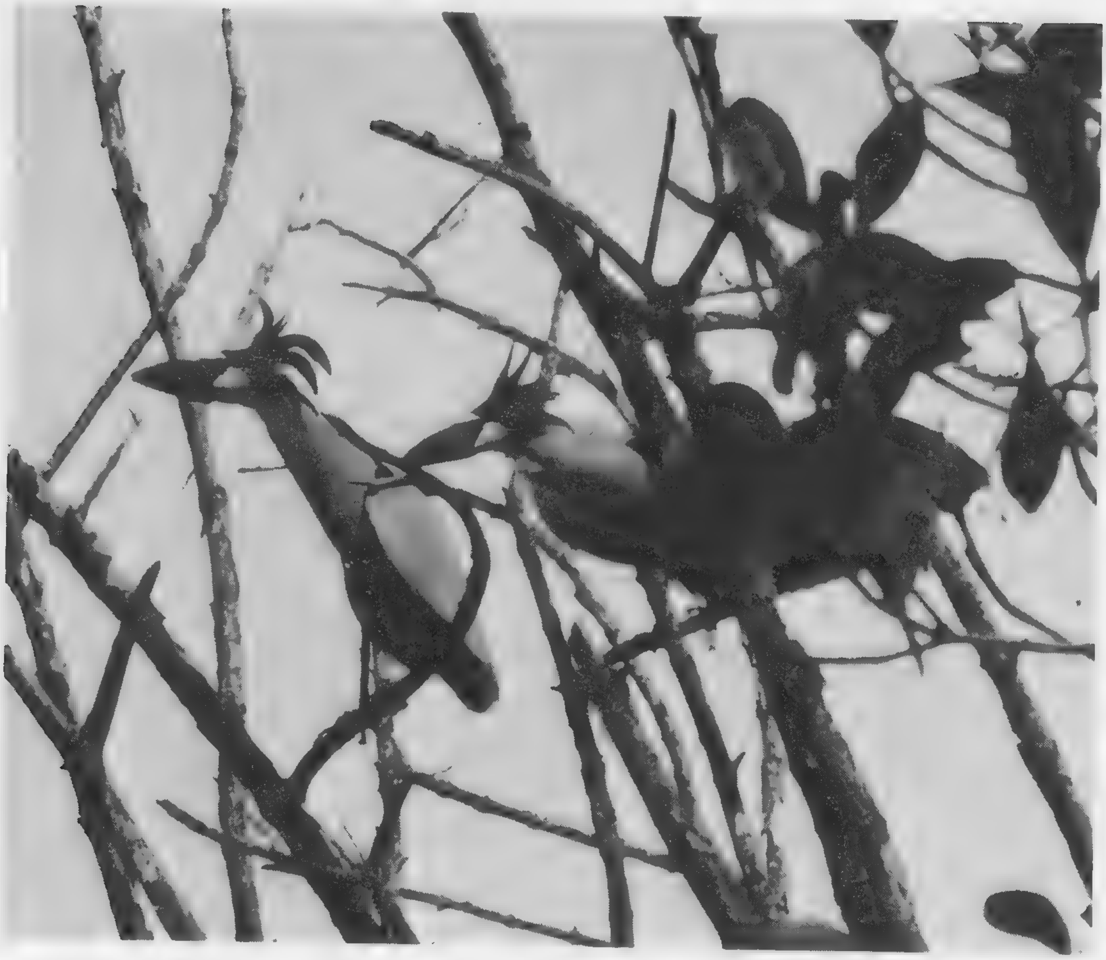


Figure 11. Long Chant being given by Boat-billed Heron (left) as conspecific lands close by.

moments of sudden excitement (e.g., as a human comes into view). Further information is needed to determine whether this is a separate display with a separate function or merely a detectable variation of the Short Chant.

Long Chant

The Long Chant differs from the Short Chant in its form, length, and contexts. It begins with an introductory phrase of several unpaired notes, like the Short Chant, then drops lower in pitch as the notes become paired. It can be either harsh or soft in tonal qualities. Frequently when this call is

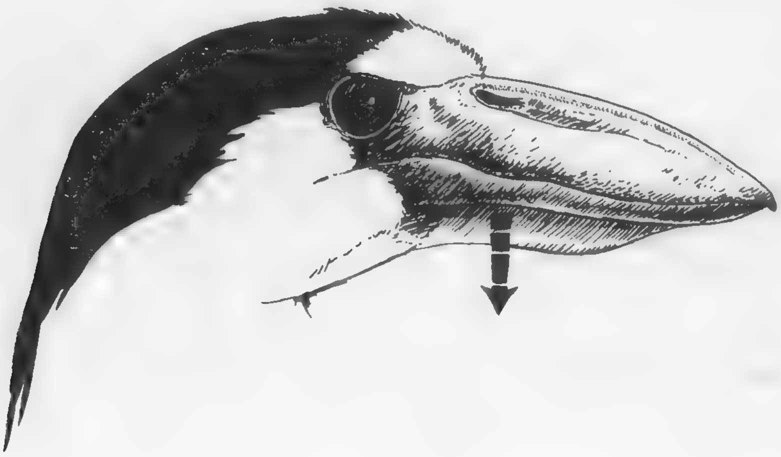


Figure 12. Drawing showing the gular distension during the Ump Call.

given by one Boat-bill, others soon join in, using distinguishably different pitches. This sometimes triggers a sequential chorus with one Boatbill after another giving Long Chants.

The Long Chant occurs during disruptions, like the Short Chant, but it is far more likely to be followed by overt attack. Long Chants are heard in the following situations: upon arrival at the territory, as a conspecific advances giving An-snaps, before Supplanting, before fights, during locomotion, while fleeing from an attack, during external disturbances (e.g., human in the colony), upon the sudden arrival of a mate on the territory (Figure 11), and, as mentioned above, after one or more neighbors have given it. On one occasion a vanquished Boatbill that had been driven into the water gave a Long Chant as it climbed out onto the prop roots. Long Chants are performed both by unpaired Boatbills and by either sex of a pair, although more commonly by the male. I believe that the Long Chant functions primarily as a restatement of territorial ownership and willingness to defend it.

Ump Call

With the bill held closed, the gular pouch stretches visibly (Figure 12), and a soft low-pitched vocalization is produced that sounds like *ump*. Sometimes the *ump* is so faint as to be scarcely audible to human ears at a distance of only 10 feet, but it can be detected by watching the throat. I have seen it given by a preening bird, a Bill-clappering pair, and a supplanted Boatbill between attacks from the aggressor. The function of the Ump Call is uncertain but may involve appeasement.

Wings Out

When a Boat-billed Heron lands on the edge of the mangroves, it usually folds its wings and walks down into the thicket. Occasionally, how-

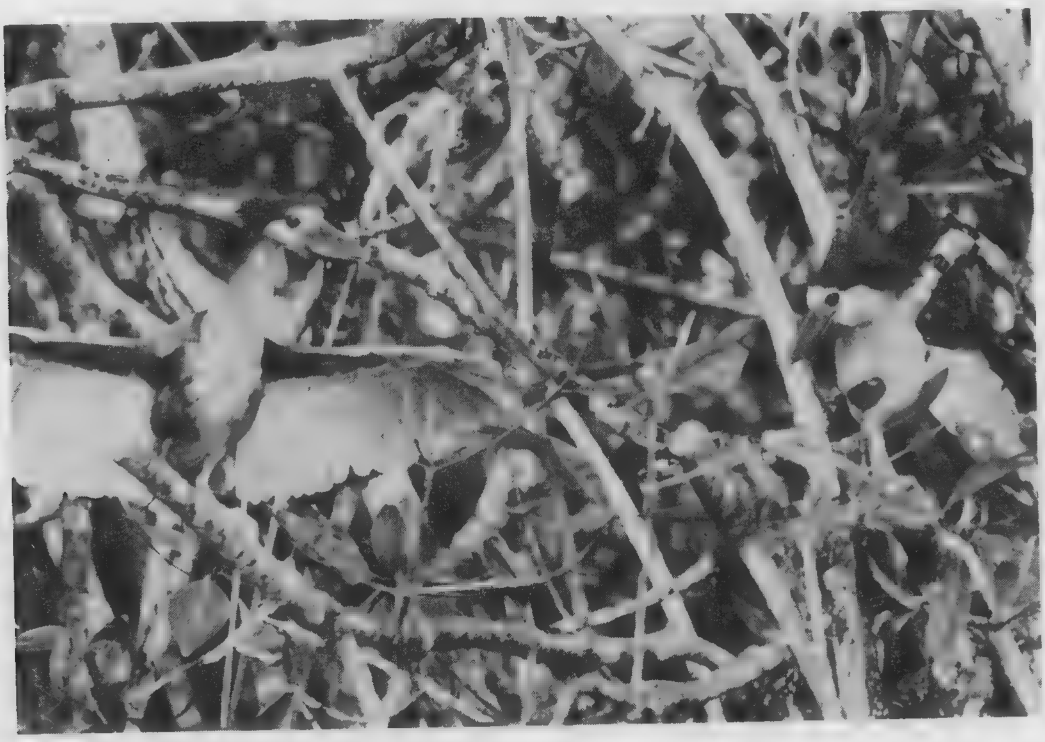


Figure 13. Wings Out performed immediately after landing at edge of mangrove thicket. Mate (on right) responds by Crest Raising.

ever, it stays at the spot of landing and holds its wings fully outspread for about five seconds (Figure 13). A bird in the Wings Out position shows no sign that it is trying to maintain balance—no compensatory readjustments or flapping. Furthermore, the Boatbill has a striking underwing pattern, a black humeral stripe that becomes highly conspicuous when exposed in this position. It seems likely, therefore, that this is a social signal that functions as a greeting ceremony to its mate or neighbors and briefly delays entry to the territory.

Pop Displays

This may represent only one display since the variations are merely in the number of bill-snaps and not in the context or the ritualized form of their performance. The double Pop is by far the most frequent type, but triple Pops, and occasionally as many as eight, are also heard (Figure 14). Triple and multiple Pops seem to increase in frequency at the time of first egg laying but more data are needed to verify this impression. If this is true, however, then the multiple Pop may well have a different meaning from the double Pop.

A typical double Pop begins as the male Boatbill walks away from his mate in a unique hunched-over position with his head lower than his shoulders (Figure 15). His walk is slow and deliberate but sometimes he hop-flies to cross gaps of vegetation. When he is one to three meters from his mate (perhaps decided by potential room for the display) he stops and displays, with the following being performed simultaneously: he (1) flexes the heels slightly; (2) snaps the head upward with the bill pointing vertically downward; (3) lowers the rump so that the torso is nearly vertical; (4) erects the occipital crest halfway; (5) flicks the wrists out and back (usually this has an amplitude of about five cm, but a full wingspread is sometimes seen); and (6) snaps the bill loudly twice (Figure 16). A sharp non-vocal noise is

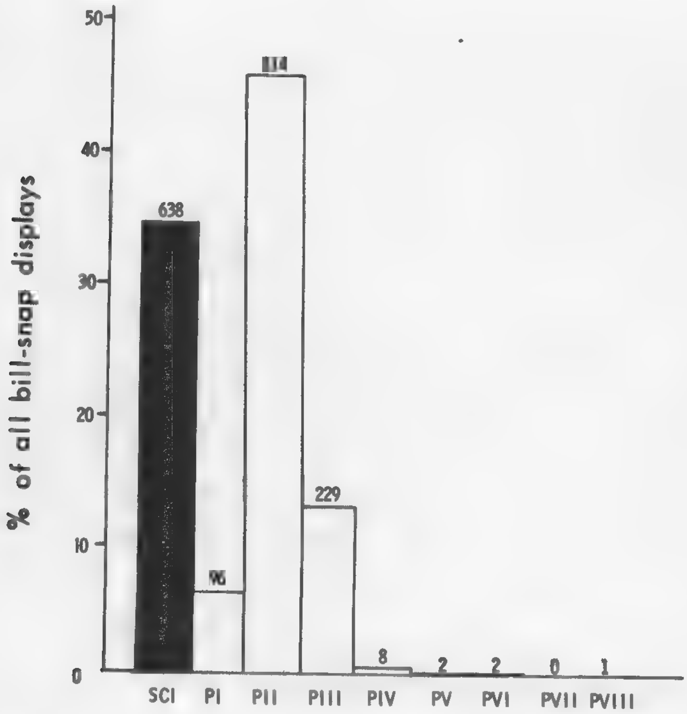
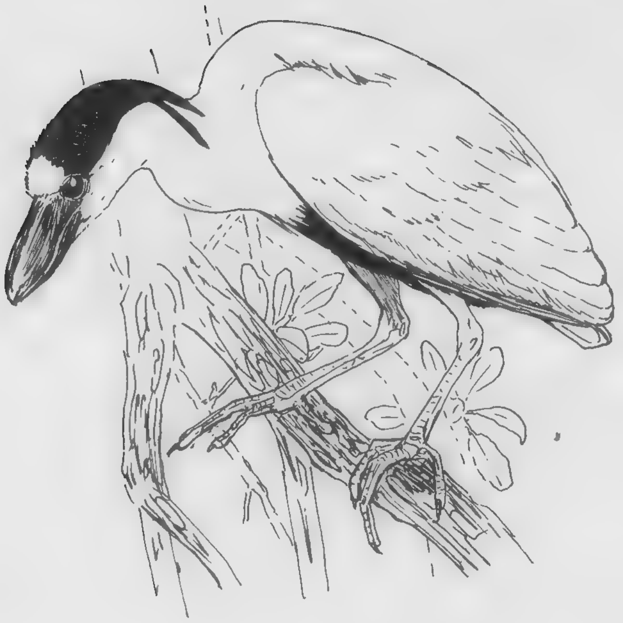


Figure 14. Relative frequencies of all bill-snap displays of the Boat-billed Heron from acoustic censuses. SCl = Single Clap. Roman numerals indicate number of bill-snaps given in Pop performances.



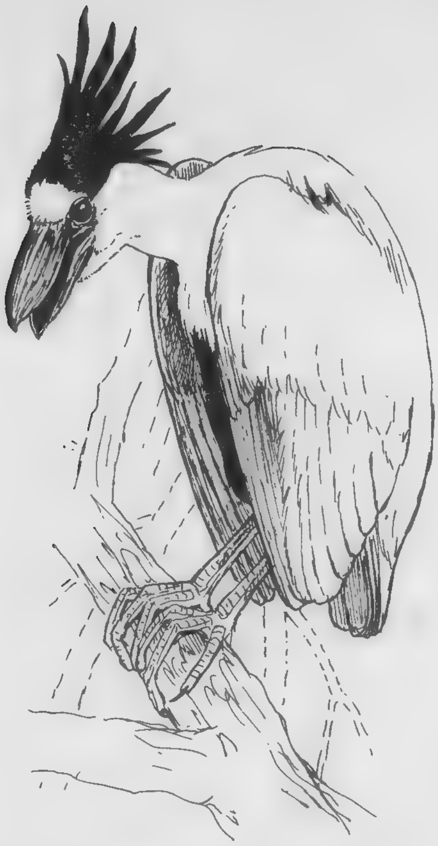


Figure 15 (*left*). Crouching walk away from mate just before performing a Pop.
Figure 16 (*right*). Form of the Pop.

produced by the mechanical impact of the upper and lower bill, and sounds very much like a very loud human handclap and probably gains resonance from the large chamber of the boat-shaped bill and flexible gular sac. Thus, although the unusual bill probably evolved primarily as a feeding adaptation (Mock, 1975), it also has a secondary function as a signaling structure.

Less commonly, males give only a single snap in this display. When it occurs with the above-described postural elements, it is probably just a variation of the Pop and is distinct from the Single Clap, which has a different form and occurs in different contexts.

Male Boatbills perform the large majority of all Pops, which occur at a rate of about three to four times per hour, but females do it occasionally also. Female Pops appear identical in form to those of the male.

A male's Pop is usually followed by contact Bill-clappering by his mate. The female either waits for him to walk back or she hurries to the performance location. When the male does a Pop without leaving the female at all, she Bill-clappers immediately. On one occasion, a female followed her mate closely when he walked off to display and Bill-clappered immediately. Even neighboring pairs may start mutual Bill-clappering after a nearby Pop.

Sometimes the Pop sound is accompanied by a vocal *an* note which may represent ambivalence about performing this display or the An-snap. More often, though, the Single Clap is used under those conditions.

The Pop probably functions as a general territory advertisement. The fact that contact Bill-clappering (appeasement function) from the mate often follows suggests that the female may need to reduce her mate's hostile tendencies after a Pop.

Displays closely resembling the Pop have not been described for any other heron species. But mechanical bill-pops are found in several heron displays that might be homologous. These displays include the Stretch of *Hydranassa tricolor* (Rodgers, 1974) and the Snap and Forward of many species (Baerends and van der Cingel, 1962; Meyerriecks, 1960). The only described bill-pop for *Nycticorax* is the Snap-Hiss (Noble *et al.*, 1938; same as "Song-and-Dance" of Allen and Mangels, 1940; and Reversed Stretch of Meyerriecks, *in* Palmer, 1962), which bears no postural resemblance whatever to the Pop. I conclude that there is no good evidence at present for any other heron display to be considered homologous with the Pop but that more information on night heron displays could re-open the question.

Single Clap

Displays involving a single bill snap occur in two forms that I believe represent different motivations and functions. One is a form of the Pop described above, having identical form and differing only in having one bill-snap. The second and far more common type (about 85 to 90 percent of all single bill-snap displays) has many similarities to the An-snap. It is this form that I refer to by the name Single Clap.

In the Single Clap, the Boatbill walks toward a conspecific, then stops, extends its neck up and forward in a stiff 45° angle, erects its crest halfway, and snaps the bill once (Figure 17). The display may be repeated one or more times with intervals of only a few seconds between performances.

Single Claps are given in territorial-defense situations. If a neighbor intrudes too close to the nest, either mate may respond with a Single Clap. It is also given by Boatbills watching others fight and may or may not be accompanied by Crest Raising then. Single Claps are quite common after landing from a short hop-flight.

An acoustic survey of all bill-snap displays was made throughout the 1974 pre-egg period in order to estimate the relative frequencies of the different displays. It was judged that between 25 and 50 pairs were sufficiently close to the blind for their loud displays to be heard; but the data are not intended to represent absolute rates of performance. Fifteen morning censuses, ranging in duration from five to twenty minutes, were made. The single bill-snap totals were corrected (because the single form of the Pop and the Single Clap *sound* identical) by a visual survey that found 85 percent to be Single Claps. The resulting frequencies are given in Figure 14.

An-snap

The An-snap closely resembles the Single Clap in form and contexts, and they may be artificial categories in a system of graded signals expressing attack tendencies. Furthermore, there is a gradient of form *within* the An-snap category that could similarly be subdivided. As a category, though, the An-snap is distinguishable from the Single Clap by (1) the presence of the loud *an* call (sometimes almost a shriek) given just as the bill-snap is made; (2) greater tendency to advance on the opponent; and (3) slightly greater erection of feathers on the neck and crest. The body is held in the same position as in the Single Clap with the neck extended stiffly upward and forward. The highest intensity performances, that is, the forms most frequently leading to all-out attacks, consist of a more horizontal posture with the wings half unfolded and, usually, rapid walking toward the opponent (Figure 18).

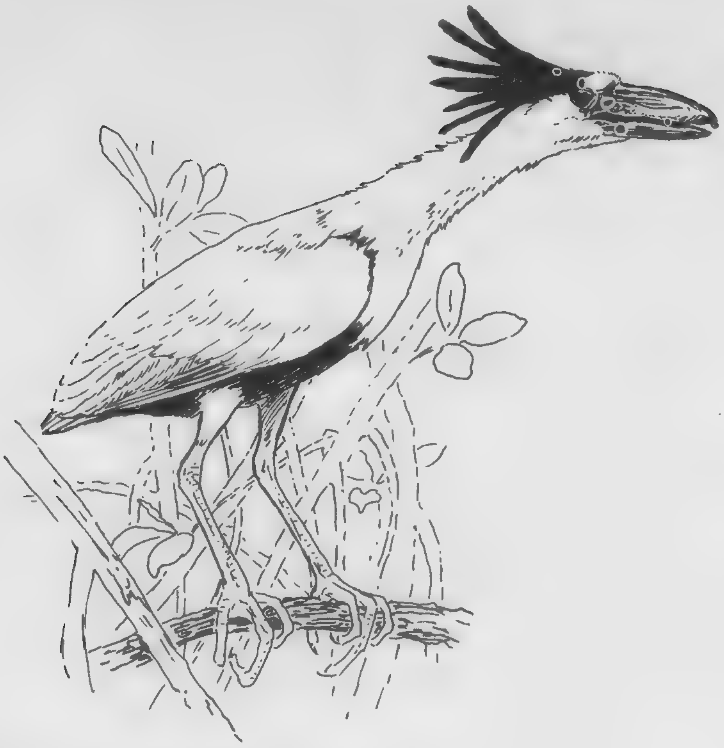


Figure 17. Form of the Single Clap and An-snap.

The three stages described above—Single Clap, high An-snap, and horizontal An-snap—are very similar to the Upright Threat, Forward, and Full Forward, respectively, found in other herons including the night herons. (Meyerriecks, 1960; Meyerriecks, in Palmer, 1962). I prefer to use different names in this preliminary descriptive account so that decisions on the displays' homologies will not be unnecessarily prejudiced. Further quantitative studies of agonistic displays of all herons are needed to determine the validity of these convenient categories in a graded system.

The contexts of the An-snap are united by the presence of a conspecific at whom the performance is oriented. This "target" (mate, neighbor, or stranger) either leaves immediately or receives a fully mobile attack (Supplant) from the displaying bird. Repeated An-snaps are sometimes given as the opponent retreats. Nearby herons who are not the "target" often give a brief Crest Raising response when an An-snap is performed. Sometimes an An-snap is given at a Boatbill in the canopy three or more meters from the displaying heron. Then the displaying bird walks in its direction, gives a tall An-snap, and ignores the "target" thereafter.

Finally, the An-snap may be the first recognizable display in a Boatbill nestling's repertoire. A human visiting the nest can elicit full An-snaps from nestlings about 14 days old. Incomplete performances, lacking the vocalization, can be elicited from nestlings about three to six days old (age estimates based on development data from Juarez and Dickerman, 1972). In nestlings, the An-snap may serve as a threat to competing siblings and as a final deterrent to predators visiting the nest.

Supplanting and Fights

All-out attacks occur in such a variety of forms, probably determined by the relative positions of the birds involved, that they are not properly considered as "displays" (they are not ritualized). However, they are an important part of the social environment of a heron colony and, as such, are included here.

Supplanting occurs when one bird charges at another and usurps its place (Figure 19). The wings are usually spread (perhaps as weapons and/or balancers), An-snaps are often given, and pecking follows if the "target" Boatbill has not fled. In the large majority of instances, the "target" retreats before actual physical contact is made; true fighting ensues only rarely. Such fights are brief, with vigorous wing-beating, stabbing, and tug-of-war contests. Once I saw a fighter knocked into the water to end a fight and, on another occasion, I saw one Boatbill seize the rump of a fleeing opponent which subsequently hung upside down in mid-air until it was released.

Overt aggression between members of a pair is rarely expressed by fighting. Usually the two mates rapidly elevate their heads, face each other, erect plumes, and may even show slight intention motions of jabbing. This "restrained fighting" subsides almost as quickly as it begins and is often followed by mutual Bill-clappering.

Miscellaneous Displays

This final section of single-bird displays presents observations that were made only infrequently but comprise a potentially important area for future study in light of the existing heron display literature.

Tail Flicking.—This has been reported in many other herons (e.g., Meyerriecks, 1960). Boatbills commonly stand in a horizontal position and move the rectrices rapidly up and down with the power stroke coming on the up-thrust. It probably communicates mild fear to conspecifics.

Head Pump.—Another simple anxiety motor pattern that may have signal value is the rapid lifting and lowering of the head. The bill is held

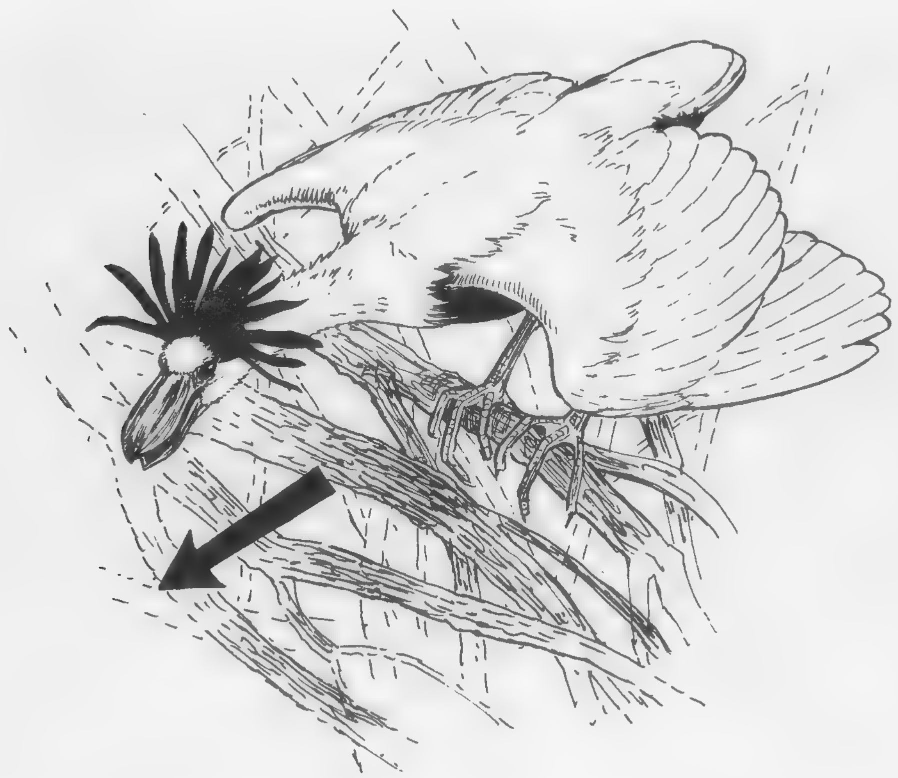


Figure 18. Horizontal advancing performance of the An-snap.

horizontally as the entire head is lifted about six cm above the shoulders. It may be performed either singly or several times in succession.

High Cry.—The highest pitched vocalizations of *Cochlearius* are made when the bird is fleeing from an attacker. These are wild squawk-like calls that may serve an appeasement function.

Wing Preen.—On a few occasions, a male Boatbill was seen to preen the leading edge of the wing one to three strokes during social interactions and following copulations. This happened so infrequently that it would probably have escaped my attention except that similar ritualized Wing Preens have been described in *Bubulcus ibis* (Blaker, 1969; Lancaster, 1970) and I have seen them also in the Great Blue Heron, Great Egret, Snowy Egret, Louisiana Heron, and Little Blue Heron. Future students of the Boatbill should watch for this motor pattern.

Pair-bond Displays

Four activities occur only within the context of an established, or establishing, pair-bond: Promenading, Bill-clappering, copulating, and nest-building.

Promenading

The male walks slowly ahead of the following female as they visit many places in the mangrove thicket (Figure 20). The two birds seem to be examining potential nest-sites as they often spend several minutes stopping at old nests and may pull at the sticks of the nest. If, during the walking, the female lags behind, the male stops and waits for her to catch up with him; mutual Bill-clappering occurs when she does. I strongly suspect that

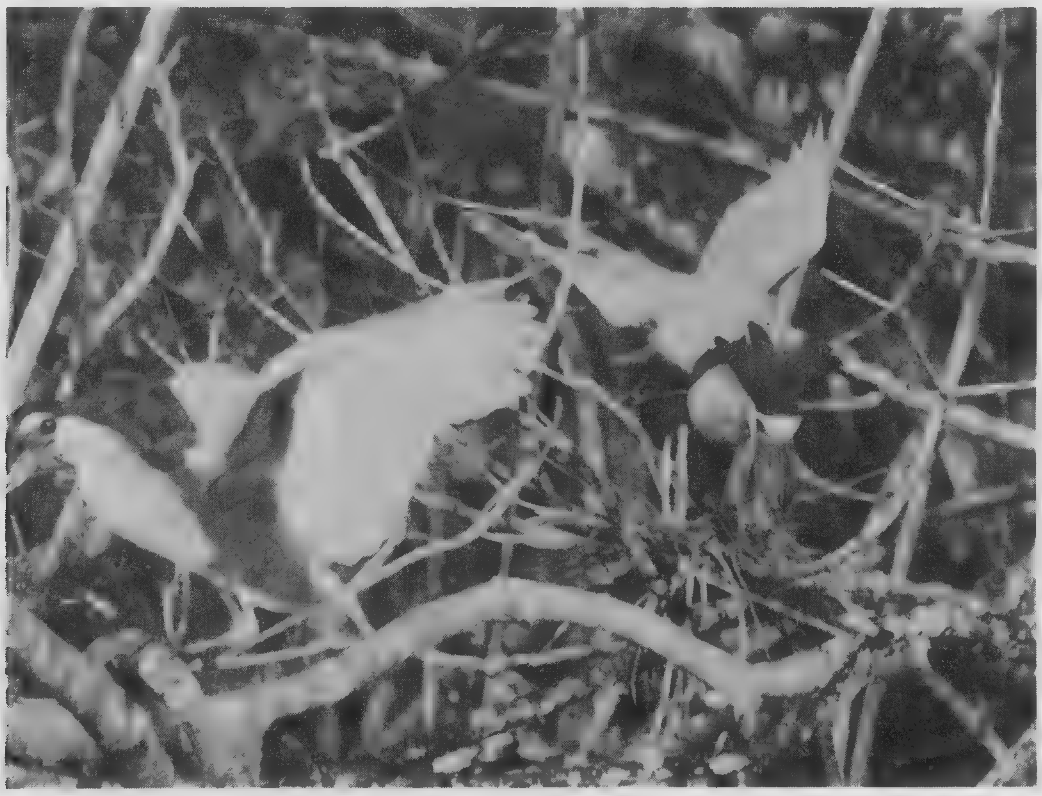


Figure 19. Nest owner Supplants a stick thief.

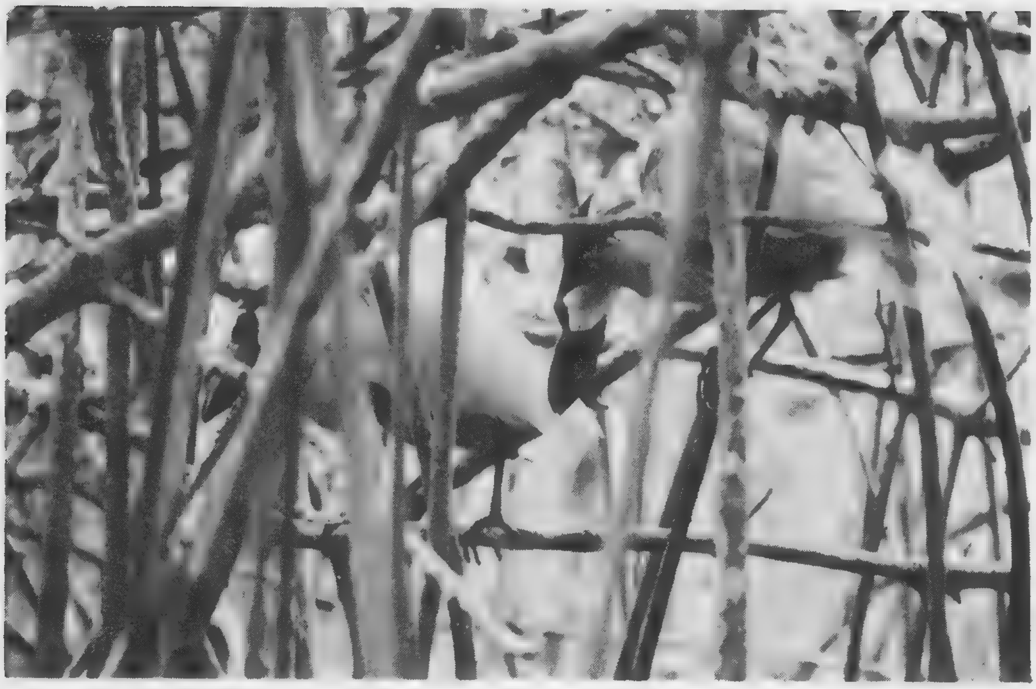


Figure 20. Promenading. Male leads the female through the colony.

this behavior marks an early stage in the formation of the pair-bond. The manner of scouting out nest-sites and frequent flare-ups of hostility between the sexes indicates a fragile balance between approach-avoidance tendencies that characterizes pair-formation in many other heron species (Meyerriecks, 1960).

Bill-clappering

In its simplest form, Contact Bill-clappering, one heron extends its neck and nibbles gently on the feathers of its mate (Figure 21). Alternatively, no actual touching may occur; then the nibbling action occurs in the air near the mate (Figure 22). This Aerial Bill-clappering may be performed by itself or it may lead to Contact Bill-clappering. In both forms, but especially in Aerial Bill-clappering, the bill produces a clicking sound audible at least 40 feet away. The click-rates of 13 taped Bill-clappering performances range from 16 to 22.7 per second ($\bar{x} = 18.8$, S.D. = 2.4). Often partial Crest Raising and/or Ump Calls accompany Bill-clappering.

Contact Bill-clappering is aimed at virtually all areas of the mate's body. Frequently one Boatbill reaches all the way over the body of its mate and Bill-clappers on the opposite side, thus increasing body-to-body contact. I observed birds receiving Bill-clappering on the back, sides, breast, rump, neck, legs, feet, head, and bill. When the legs or feet are Bill-clappered there is an increased likelihood that mutual Bill-clappering will follow. Other heron species tend not to Bill-clapper the bill itself, but the Boatbills do it in a variety of ways involving the entire bill, the tip only, and even the bill when open. This, and other lines of evidence (such as bill scratching), suggest that the bill in *Cochlearius* is more touch-sensitive than that of other herons.

Bill-clappering is by far the most common Boatbill display and can occur any time a pair is together. Although it may occur when the birds are totally quiet, it is more often elicited by movement on the part of the receiver. It is most common after one member has participated in a social interaction with another conspecific, and especially after aggression (An-

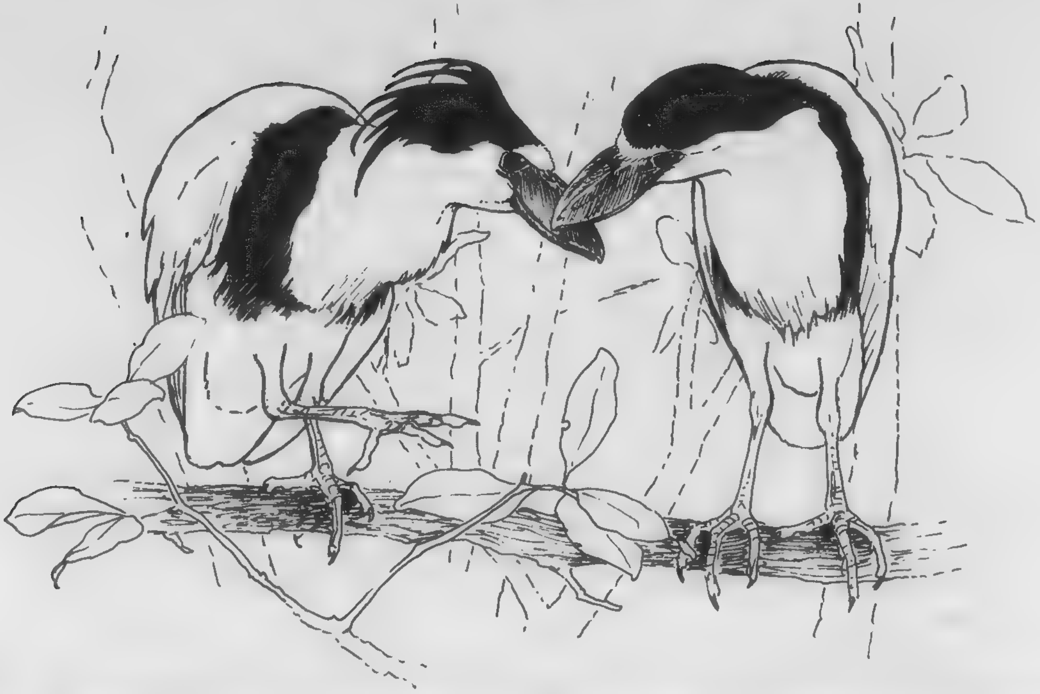


Figure 21. Contact Bill-clappering on mate's bill. This supports the suggestion that *Cochlearius'* bill is more touch-sensitive than the bills of other herons that do not use their bills as targets for Bill-clappering.

snaps, Pops, fights, and Tall Rocking). Hostile interactions between the mates are almost always concluded with mutual Bill-clappering. Generally, Bill-clappering is elicited by alarm situations or sudden changes in the receiver's behavior. Although either sex may initiate Bill-clappering, the male seems to start it more than the female.

Bill-clappering presumably evolved from nonritualized allopreening (Hudson, 1965) and appears to function as an appeasement signal just as allopreening does in other birds (Harrison, 1965). The display was thoroughly described for the Grey Heron by Hudson (1965) and has since been recorded in the Cattle Egret (Blaker, 1969; Lancaster, 1970), Louisiana Heron (Rodgers, 1974), Little Blue Heron, Great Egret, and Great Blue Heron (Mock, pers. observ.). In these last three species, at least, it resembles the Boat-bill's version exactly (both aerial and contact forms) with the exception of mutual Bill-clappering on the bills in *Cochlearius.*

Copulation

Boat-billed Heron copulation is usually preceded by mutual Bill-clappering accompanied by bodily contact, such as the male leaning on the female. Then the male steps directly onto the female's back, flapping his wings for balance. Once on top, he turns parallel with her and tries to get a foot-grip on her wings while resting on his heels. The female cooperates with the mounting effort by assuming a horizontal stance, bracing her feet more widely, and lifting her partially extended wings out to form a broader platform (Figure 23). Rarely, she delays her cooperation until the male has already settled on her back. Once steady, the male lowers his rump to one side of the female's tail and pushes it sideways to establish cloacal contact. The male Boat-billed Heron does not grasp his mate's head during copulation as in a few other heron species (e.g., *Ardea herodias).* Actual cloacal contact is brief, four to eight seconds. Then the male dismounts and either stands quietly next to the female or moves a short distance away for one or more

Pops. One male immediately began an active solo session of nest building immediately after a copulation.

During some copulations, the male emits a distinctive Copulation Call. This consists of triplets of notes with the middle note higher in pitch (each note can best be represented using the International Phonetic Alphabet: *Ɛn*). The call is given rapidly with two triplets and their intervening pause taking only about 1.5 seconds altogether.

Copulations occur in a variety of places in the colony vegetation. Most are performed on the nest or nest-site, but some occur more than two meters over the water, just under the canopy.

Feeding Niche

The unusual bill of the Boat-billed Heron presumably evolved during a shift of the feeding niche. Several lines of evidence suggest that the bill is a touch-feeding adaptation that permits efficient exploitation of a temporary food abundance during the nesting period (Mock, 1975). This conclusion is based on several points: (1) The nesting of Boatbills is timed to coincide with the rainy season flooding of shallow brackish lagoons (Dickerman and Juarez, 1971). At the same time shrimp and other marine organisms enter the lagoons to molt and reproduce. This provides an ephemeral abundance of food. (2) Thirteen breeding adult Boatbills were collected and their stomach contents examined. These stomachs contained only four prey species, all of whom inhabit submerged mud, plus considerable amounts of mud. (3) In San Blas, the Boatbills foraged only at night during the rainy (nesting) season. Thus there is little available moonlight penetrating through the overcast night skies. And they even seem to avoid what little moonlight there is by feeding under mangrove foliage. (4) The bill of *Cochlearius* appears to be more touch-sensitive than the bills of other herons, reflected in the higher frequency of comfort scratching and social Bill-clappering on the bill.

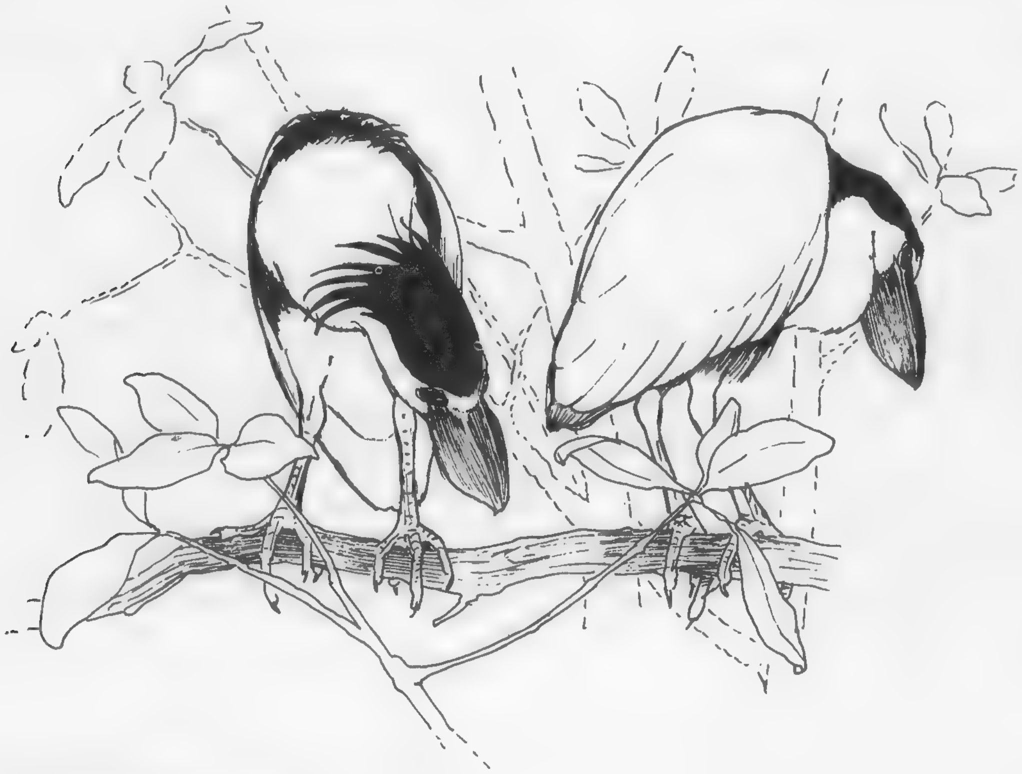


Figure 22. Aerial Bill-clappering near mate's rump.

Therefore, because the breeding Boatbills are catching prey in a soft, opaque medium (mud) on dark overcast nights, I conclude that they cannot be using vision effectively for hunting. Touch-feeding with a sensitive bill, by contrast, would ideally suit these conditions. Also, touch-feeding would be enhanced at least two ways by evolving a wider bill: (1) the total capture-surface would be increased, providing a "catcher's mitt" advantage, and (2) rapid opening of the bill could create a partial vacuum to draw prey items (and mud) into the mouth.

Although Boatbills are capable of hunting visually (Carpenter, 1971; Mock, pers. observ.; Wetmore, 1965), this must be an inefficient system for getting the lagoon's food supply during the breeding season. Yet the stomach analysis shows that they are eating these items in quantity. It is likely, then, that *Cochlearius* uses a special touch-feeding method during the nesting period although it may use a variety of techniques the year round, as other herons do (Meyerriecks, 1962).

Displays and Habitat

Boat-billed Herons nest in denser thickets of vegetation than any other heron known. In the maze of mangrove prop roots, they gain several potential advantages: (1) Their nests are concealed from diurnal predators. By contrast, the hundreds of nearby Great and Snowy Egrets and Louisiana and Little Blue Herons have exposed nests and suffer egg predation from local humans. (2) They are in the middle of a wide body of water that renders them less accessible to ground predators. (3) They are sheltered from the thermal stresses of tropical sun and chilling rains. (4) Their large, night-adapted eyes are shaded from the midday brightness. (5) They are situated in the center of their feeding habitat. For all these benefits, they are also uniquely restricted in the kinds of social signals they can use, the physical movements they can make, and by the fact that they must defend three-dimensional territories instead of the two-dimensional territories of open-nesting herons.

Perhaps because of these habitat differences, *Cochlearius* has evolved a repertoire of social displays quite different from that of other herons studied to date. Aerial displays, for example, seem to be absent in the Boatbill repertoire—not surprising for a species living in a roofed colony. And there is much more vertical climbing space from which to display within the chamber-like internal structure of the mangrove thickets (Figure 24). Also, compared to other herons, they rely far more heavily on acoustic signals than visual signals—a strategy used by many animals inhabiting dense environments where sound waves penetrate the vegetation more efficiently. Nearly all of *Cochlearius'* display postures and movements are reinforced with an acoustic component: the visual components are probably effective only at short range. Furthermore, Boatbills produce mostly low-pitched vocal and mechanical sounds, which penetrate dense vegetation better than high-pitched sounds (Morton, 1975).

Comparative studies of other herons nesting in moderate vegetation density should be made to further elucidate the impact of environment on heron communication.

Behavioral Characters and Taxonomy

The behavioral repertoire of *Cochlearius* is similar to that of other herons in such categories as locomotion and comfort activities, but is unique

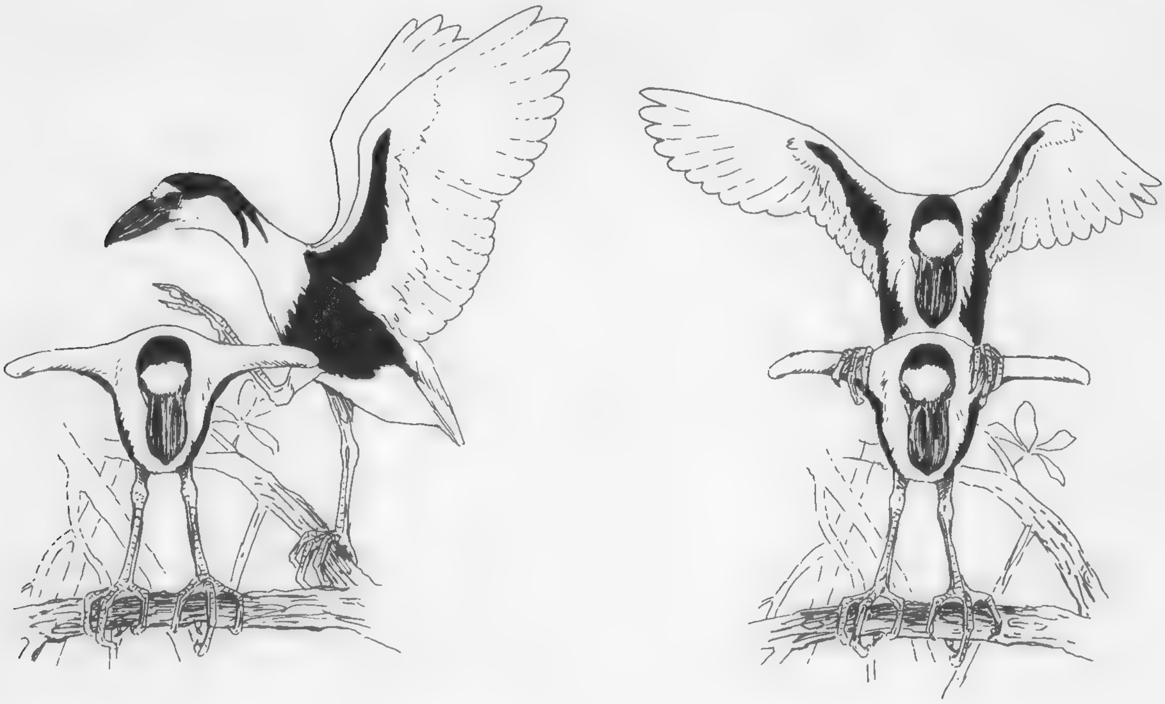


Figure 23. Copulation. The female assumes a horizontal posture and lifts her wings as the male mounts. The male then grips the female's wings with his toes during cloacal contact.

among herons in social displays. The distinctively tangled colony habitat obviously has made strong demands on the form of display signals. And only two of the 12 most common displays described in this paper are clearly identical in form with known displays in other herons (Crest Raising and Bill-clappering). In addition, there are four less frequent signals that may also represent shared primitive character-states: Scapular Erection, Twig-shake, Tail-flicking, and Wing Preen. The case for homologizing Crest Raising and Bill-clappering is strengthened by the fact that they have not been found in other families of Ciconiiform birds. Furthermore, both of these are short-range displays and thus less subject to habitat interference. I conclude that at least these displays are homologous with ardeid displays in the evolutionary sense of common phylogeny. The importance of the other ten displays must be tempered by the consideration of *Cochlearius'* nesting habitat. I believe they may have evolved very rapidly. And the non-display behavior appears unchanged over the span of genetic isolation.

I conclude that the ethological characters for *Cochlearius* are about as perplexing as the earlier taxonomic characters, with both striking similarities and dissimilarities between the Boatbill and the other herons. *Cochlearius* is obviously closely related to other herons, especially the night herons. But the many dissimilar characters, including egg color, powder-down patches, natal plumage, and now social behavior should be reflected in any classification. I prefer to emphasize the similarities by placing *Cochlearius* in the tribe Nycticoracini but acknowledge the choice of others to distinguish *Cochlearius* with its own tribe.

An Evolutionary Scenario for *Cochlearius*

A population of ancestral night herons became geographically isolated in the neotropics. There it underwent an ecological shift, gradually becoming better adapted to exploit the rich but ephemeral food source provided by flooding of seasonal lagoons. This new feeding niche led to modifications in breeding season timing (synchronizing with lagoon flooding), and vision (increased sensitivity for nocturnal activity). In turn, the new feeding niche led to the use of a new nesting habitat that was more sheltered and better camouflaged from predators. This nesting habitat change caused substantial alterations on the displays used in the colony, favoring signals that penetrated vegetation well (Figure 25).

Summary

During the summers of 1973 and 1974 the behavior of the neotropical Boat-billed Heron *(Cochlearius cochlearius)* was studied in a colony near San Blas, Nayarit, Mexico. Descriptions of locomotion, comfort activities, and social behavior are presented here. Generally the locomotory and comfort behavior patterns of this species agree closely with those of other ardeids but the social displays are surprisingly dissimilar. Only two of the twelve most common Boatbill displays (Crest Raising and Bill-clappering) are clearly homologous with other known heron displays. These repertoire differences are discussed in light of the Boat-billed Heron's much denser nesting habitat (mangrove prop roots and stems) where selection for non-visual

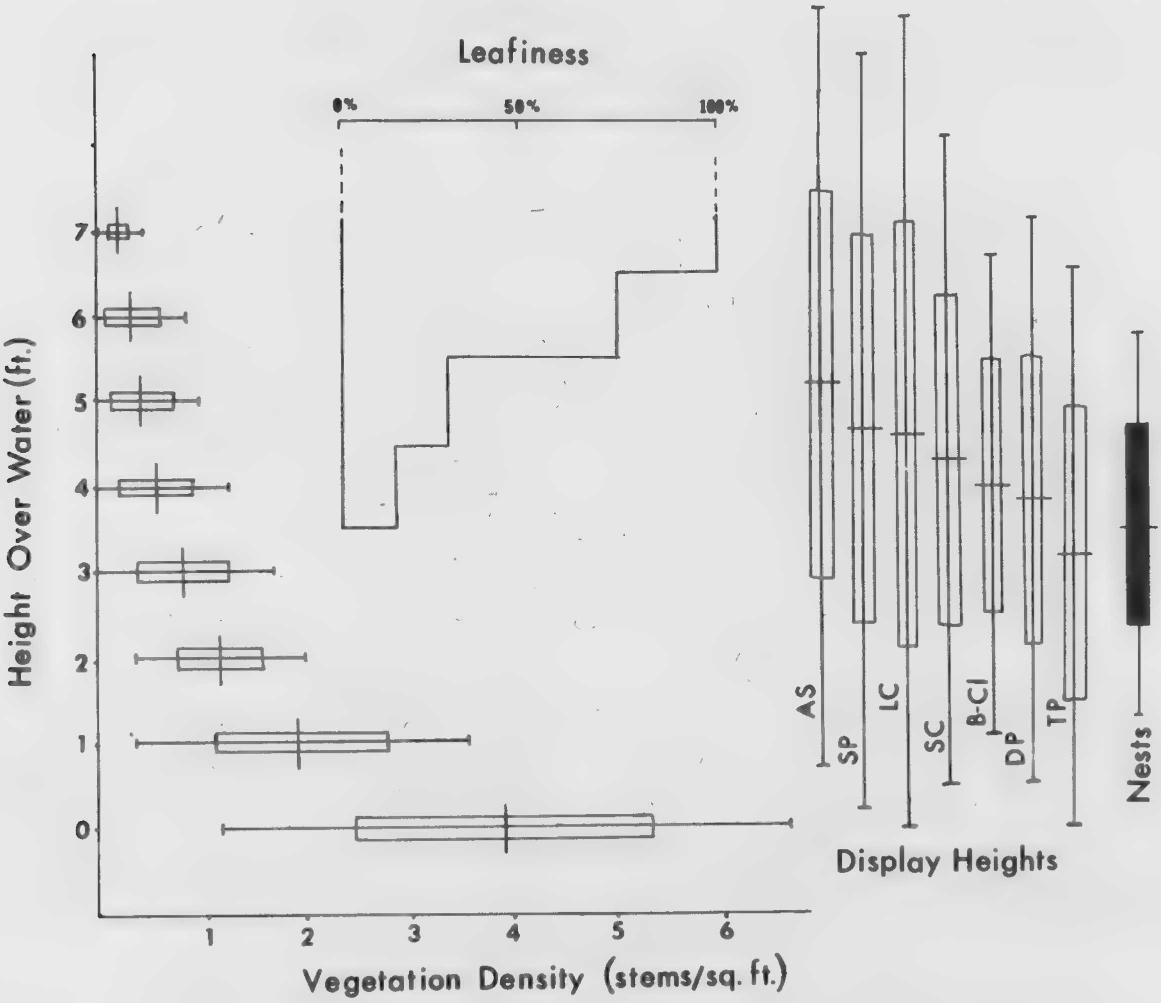


Figure 24. Physiognomic characteristics of the colony's mangroves with Boatbill display and nest heights shown. "Leafiness" indicates percentage of sampled quadrats whose foliage canopy begins at the designated heights above water. Displays are coded as follows: AS = An-snap (n = 96), SCl = Single Clap (n = 74), LC = Long Chant (n = 87), SCh = Short Chant (n = 70), B-Cl = Bill-clappering (n=81), DP = double Pop (n=90), and TP = triple Pop (n=11).

signals would be expected. Thus the Boatbill has apparently diverged from other herons in evolving a much more acoustic repertoire of displays. The extra wide bill is considered as a probable touch-feeding adaptation that enables the herons to efficiently exploit the sudden influxes of mud-dwelling marine organisms in the temporary lagoons. This ephemeral abundance of prey items seems to trigger nesting in the Boatbills which begin building nests as the lagoons flood early in the rainy season. A speculative evolutionary history for *Cochlearius* is proposed.

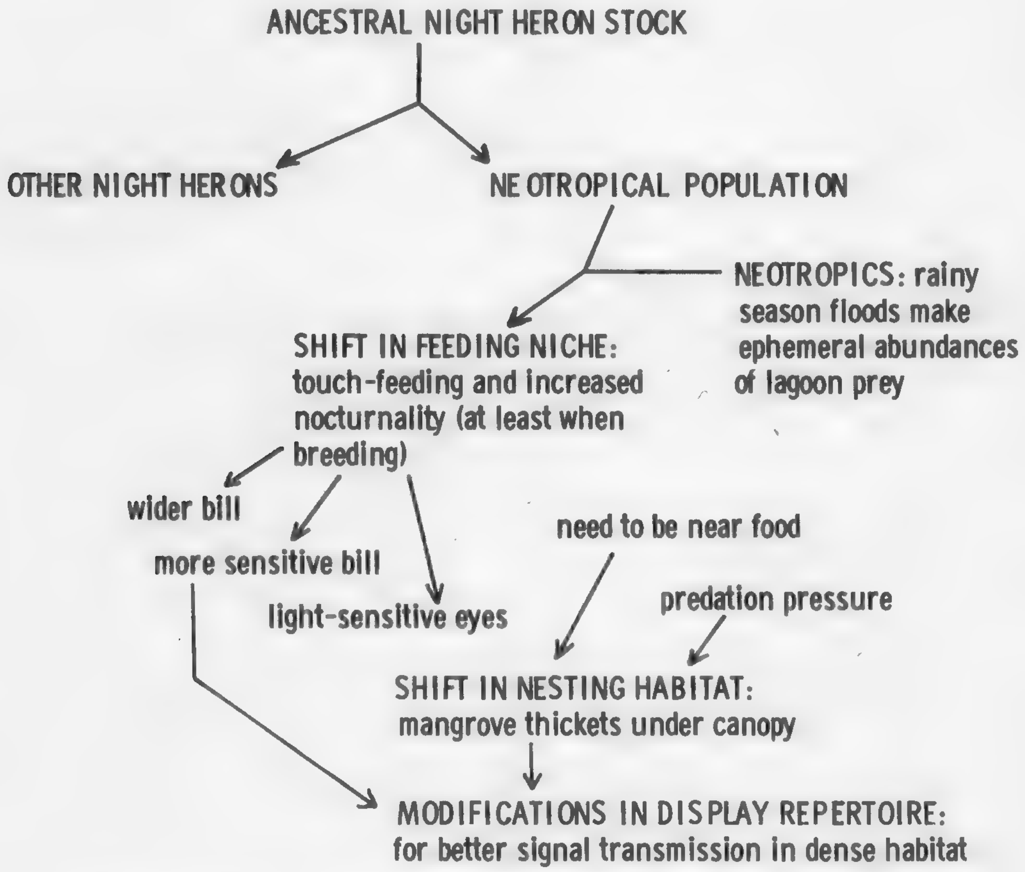

ANCESTRAL NIGHT HERON STOCK
OTHER NIGHT HERONS
NEOTROPICAL POPULATION
NEOTROPICS: rainy season floods make ephemeral abundances of lagoon prey
SHIFT IN FEEDING NICHE: touch-feeding and increased nocturnality (at least when breeding)
wider bill
more sensitive bill
light-sensitive eyes
need to be near food
predation pressure
SHIFT IN NESTING HABITAT: mangrove thickets under canopy
MODIFICATIONS IN DISPLAY REPERTOIRE: for better signal transmission in dense habitat

Figure 25. Suggested history for the evolution of *Cochlearius* with major ecological shifts and selective forces indicated.

Acknowledgments

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Carolina Wren, *Thryothorus ludovicianus*. Drawing by John A. Ruthven.

COURTSHIP BEHAVIOR OF THE GREATER ROADRUNNER

MARTHA WHITSON

Although the Greater Roadrunner, *Geococcyx californianus* (Family Cuculidae), is a popular and conspicuous bird of the southwestern United States and Mexico, the literature contains little information about its courtship behavior. A single field observation of copulation (Rand, 1941) and a brief account of breeding of a hand-reared pair (Calder, 1967) contain all the information available on the courtship of the Greater Roadrunner.

I investigated the courtship behavior of the Greater Roadrunner, hereafter referred to as the Roadrunner, in both wild and captive situations in order to (1) describe the behavior patterns, (2) quantify these descriptions as much as possible, (3) investigate time-motion patterns of behavioral sequences, (4) understand the functions of these behaviors, (5) delineate changes in the courtship pattern during the breeding cycle, and (6) trace the development of courtship behavior in juveniles.

The breeding range of the Roadrunner extends from Kansas (Prophet, 1957) and California (Kimsey, 1958) south to Baja California and east and south over the Central Plateau of Mexico (Blake, 1953). The species inhabits a variety of habitats throughout its range (Behle, 1960; Dixon, 1959; Hamilton, 1962). It occurs most commonly in marginal areas of mixed open land and brush or forest, and rarely in the extremes of either sparse or dense vegetation (Grinnell and Miller, 1944; and Whitson, pers. observ.). Double-broodedness is common (Sutton, *in* Bent, 1940; Woods, 1960) and triple-broodedness occurs occasionally (Whitson, pers. observ.).

This paper reports on the courtship behavior of both captive and wild birds observed from 1966 to 1972. I found acoustic behavior to be the prominent feature of courtship, a more detailed discussion of which is planned for subsequent publication.

Methods

Study Areas

I carried out my investigation on study areas in Karnes and Starr Counties in south Texas, in Big Bend National Park in west Texas, in Marshall County in south central Oklahoma, in Cleveland County in central Oklahoma, and in Doña Ana County in southern New Mexico. A detailed description of the study sites is presented elsewhere (Whitson, 1971).

Observations

Observations were made with 7 x 35 binoculars and a 5-60X zoom spotting scope. I never used a blind in the field, and the birds readily adjusted to my presence. I usually began my observations from 20 to 30 meters away, daily reducing this to a final viewing distance of 10 to 15 meters. I spent approximately 1,015 hours in field observations from 1966 to 1972.

Plumage variations commonly distinguished individual birds and usually were due to loss of conspicuous feathers, especially the white-tipped rectrices (Figure 1). As I noted no apparent anatomical differences between mated birds, sexual identification was not always possible. In those pairs observed for extended periods, I distinguished sexes behaviorally, with final criteria being the relative position during copulation or egg-laying. A subsequent study (Folse, 1974) describes a sexual difference in the color of the postorbital apterium, which could be useful for future field identification of the sexes.

Juveniles were distinguished from adults by mouth color. The mouth of the young Roadrunner is pink for the first 50 to 55 days of life, then gradually becomes speckled until, at the age of 80 to 85 days, the mouth lining turns completely black (pers. observ.). I made this distinction in wild birds as they fed, panted, and yawned.

The orbital skin in adults is blue dorsally and ventrally. The anterior portion of the postorbital apterium (unfeathered region behind the eye) is also blue dorsally and ventrally, but pale blue (female) or white (male) immediately behind the eye (Folse, 1974). The posterior area is a bright orange in both sexes. The orbital skin is always exposed, but the postorbital apterium is normally completely obscured by feathers (Figure 2A). The apterium becomes exposed during courtship to varying degrees (Figures 2B-2G). The exposure of the postorbital apterium is not dependent on the erection of the crest.

I observed 14 wild pairs during all or part of their breeding season, as well as numerous single Roadrunners. An outdoor enclosure (9 x 9 x 4 meters) at the Animal Behavior Laboratory, University of Oklahoma housed captive birds. I raised two birds in my residence. I observed eight hand-reared birds, seven of which were taken from the wild as 5- to 15-day-old nestlings. The eighth was artificially hatched and completely isolated from other Roadrunners until adult. The captives exhibited courtship displays to humans, providing excellent opportunities for close-range observation of behavior. I observed the captives for approximately 500 hours during the breeding season.

Film Analysis

I filmed courtship displays of captive and wild birds with a Model H-16 Bolex 16mm movie camera and a 17-85 Pan Cinor zoom lens. Filming speeds were 18 or 24 feet per second. Usng a Bell and Howell Model 173 Time and Motion Study Projector, drawings from successive frames were superimposed to obtain time-motion descriptions of behavioral sequences, with a temporal resolution of 1/18 or 1/24 second. Analyses included approximately 4,500 frames of wild bird behavior and 6,500 frames of captive bird behavior.

Acoustic Analysis

Acoustic signals were recorded with a Uher 4000 Report L portable tape recorder and an omnidirectional microphone. I analyzed the recordings by ear to determine the number of notes per call and also performed a sonographic analysis, which will be presented in a subsequent paper. I have described each signal by an onomatopoetic name, retaining those terms already in literature where applicable.

Courtship Behaviors

The various Roadrunner courtship behaviors are described and illustrated (Figures 3 to 11) below. Unless otherwise stated, I described the displays from films of captive and wild birds, and noted no differences between these two groups. Since I will refer frequently to movements and positions of certain body parts in describing behaviors, the reader should refer to Figure 1. I used the method employed by van Tets (1965) in describing the position of the tail.

Particular feather patterns appear when tail or wings are held in certain

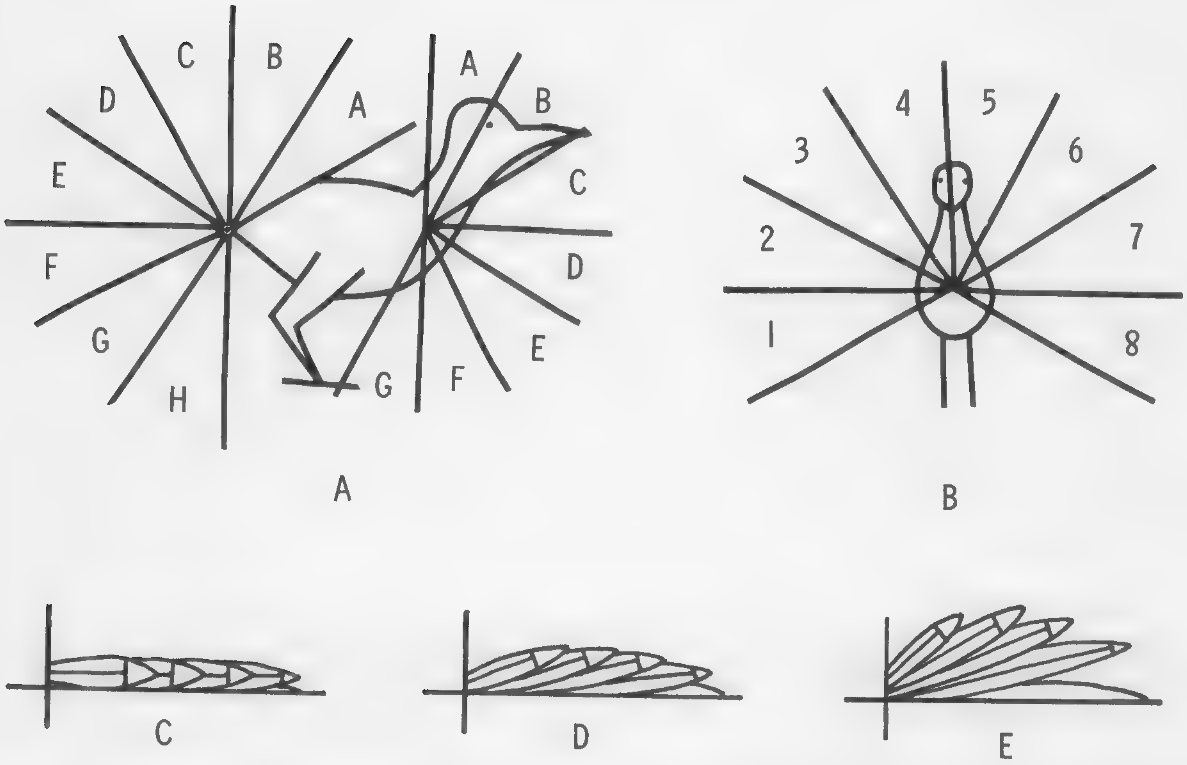


Figure 1. Tail and head positions used in descriptions of courtship. (A) Sectors for head and tail postures, side view; (B) sectors for tail postures, anterior view; (C) ventral tail, closed; (D) ventral tail, moderately fanned; (E) ventral tail, fully fanned.

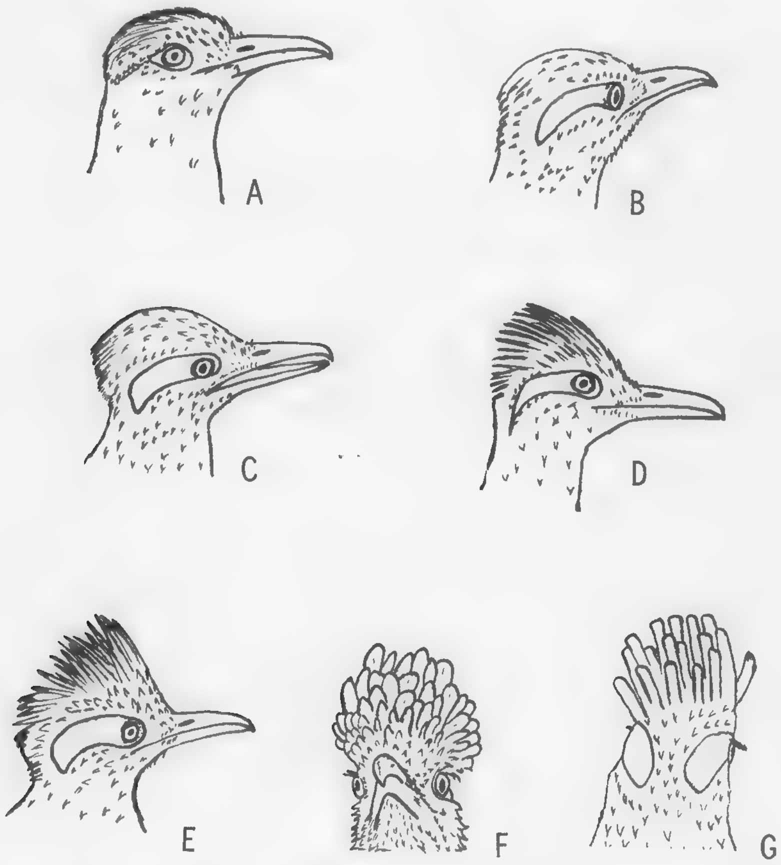


Figure 2. Crest positions and degrees of exposure of the postorbital apterium. (A) Crest normal, apterium obscured; (B) crest sleeked, exposed apterium; (C) crest slightly erect, apterium exposed; (D) crest moderately erect, apterium partially obscured; (E) crest fully erect, apterium fully exposed; (F) anterior view of E; (G) posterior view of E.

positions. Thus, the white tips of the lateral rectrices are visible from a frontal view only during tail-fanning. The small white spots on the remiges are exposed during wing-dropping.

Acoustic Signals

I recorded nine acoustic signals during courtship. These are summarized below and will be discussed more thoroughly in a subsequent paper.

Coo. — The Coo, produced only by the male, consists of from three to eight low frequency, downward slurring notes. It resembles the cooing of a dove, and is audible to about 250 meters. It is most frequently given from an elevated perch in the early morning.

Head movements accompanying the Coo are conspicuous and exhibit a temporal pattern (Whitson, 1971). From the normal position the head is lowered with the crest fully erected and the apterium exposed (Figure 3). The bill is then moved away from the body as each note is made, and brought nearer the body before the next note begins. The first note is always the shortest note, the last note always the longest. A typical five-note call would be : *co-coo-coo-coo-coooooo*. The male often gives the Coo call for as long as an hour, from the same perch or from different ones.

Short Coo. — Similar to the Coo, but consists of two notes, the first one always shorter than the second: *coo-cooooo*. It is rarely given, produced only by males, and can be heard up to 30 meters away. Head movements accompanying this call are similar to those described for the Coo. Unlike the Coo, however, Roadrunners render the short Coo only from the ground, and only for short periods of time.

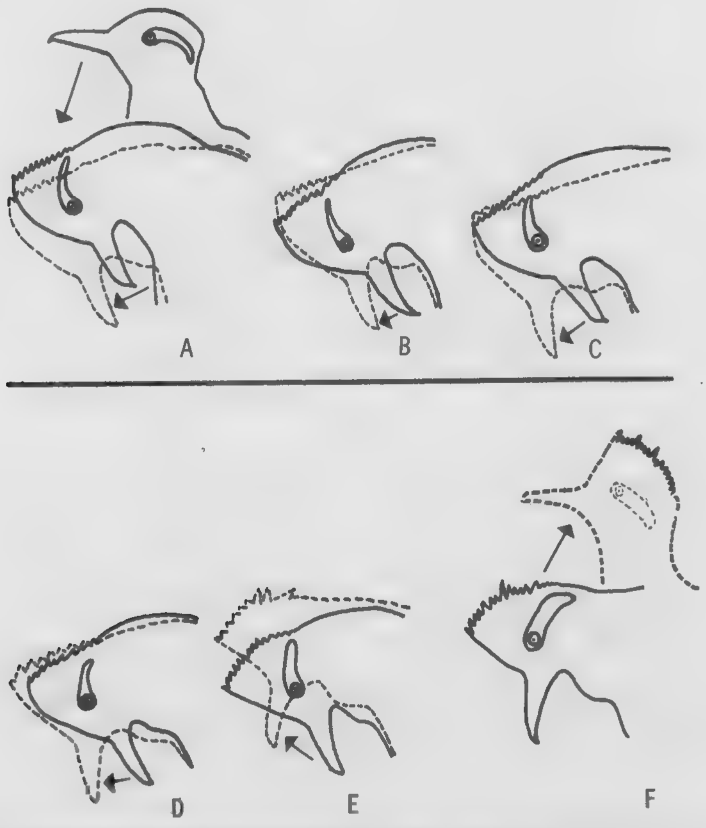


Figure 3. Head movements of a six-note Coo call. Each drawing represents the production of one note. The solid line depicts the head just before the note begins and the dotted line depicts the head's position at the end of the note. The solid horizontal lines serve as reference points to note the slight head lowering with each of the early notes.

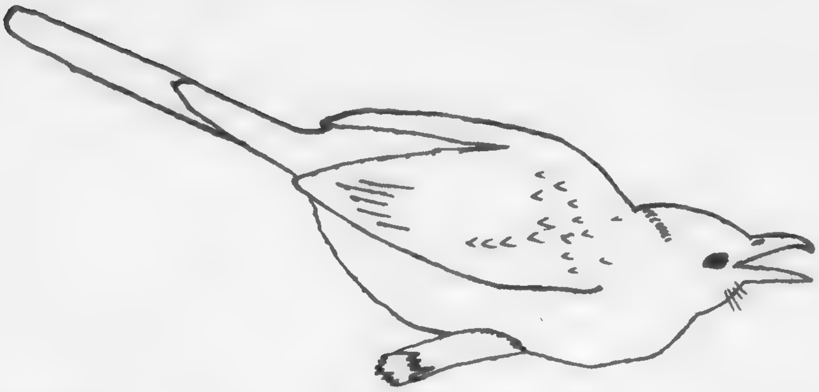


Figure 4. Posture of a female as she emits the Whine vocalization.

Single Coo. — The Single Coo consists of one very soft note, similar in tonal quality to the Coo notes, but with no downward slurr. It is given by both sexes and always accompanies the Flick-bow behavior described below. It can be heard at a distance of only two meters from the calling bird.

Bark. — A rapid series of sharp, short, low frequency notes, varying from 2 to 22 in number, and resembling the barks or yelps of coyotes. I heard only females give this call, with the exception of one wild male. The call can be heard 300 meters away. With each Bark note, the bird's body jerks slightly and the bill is opened a bit. Crest postures vary from normal to slightly erected, and the apterium is exposed to a greater or lesser degree.

Clack. — A sharp, clacking noise produced by the mandibles snapping rapidly together, accompanied by a simultaneous vocal whine. The average Clack consists of five notes (range 1 to 12) and varies in loudness, being heard up to a distance of 200 meters. While calling, the bird stands erect with crest slightly or fully erected and the apterium slightly to fully exposed. Both sexes produce the Clack, although I detected a sexual difference in pitch; the female has a somewhat higher pitched Clack. It is the most frequently heard sound, both during the breeding and nonbreeding seasons.

Growl. — A low frequency growling sound of three to four notes, given by both sexes, and heard up to 15 meters away. As each note is produced, the throat bulges conspicuously. The bird stands with feathers slightly fluffed, crest fully erected, and postorbital apterium partially obscured.

Whirr. — The Whirr consists of a steady stream of soft, low frequency putting sounds, regularly interspersed with a slow, whirring sound. The effect is a mechanical sounding noise that can be depicted as *putt-putt-putt-putt-whirrrrrr-putt-putt-putt-putt-whirrrrrr.* Given only by the male, this call always accompanies the Tail-wag display described later. The sound carries up to two meters from the source.

Whine. — Consists of one long, low frequency whining sound. The note is often repeated for periods as long as five minutes and is given by both sexes, usually from a sitting or crouching position (Figure 4). The head moves in a vertical plane from sectors B to E or F. From three to six horizontal head-shakes are given during the downward movement. Initially, the bill is open at a 50- to 60-degree angle as the Whine is being made, but gradually closes as the head reaches the lowest point of the vertical movement. The feathers and crest are sleeked and the postorbital apterium is obscured. The call is soft and carries for a distance of only five meters.

Pop. — A series of four to eight sharp, loud popping noises produced by the wings during the Prance display described later. Given only by the male, the Pop can be heard 30 meters away.

Chase

A vigorous ground chase often lasts for several hours, with both birds stopping frequently to rest. The fast running is interspersed with low gliding flights. Occasionally the pursuing bird attacks with wings and tail raised and fanned (Figure 5). During intervals between chases, both sexes frequently give one or more displays, including the Coo, Bark, Clack, Tail-wag, Stick-offer, Growl, Whine, Flick-bow, and Single Coo.

Stick-offer

During the Stick-offer, one bird approaches with a stick or blade of grass in its bill and drops it a few centimeters in front of its mate or transfers it to the latter's bill.The displaying bird often shakes the grass or stick and throws it down in front of its mate in a manner similar to that of food treatment for this species. Both sexes exhibited this behavior, and often accompanied it with other courtship behaviors.

Prance

Only males manifest the Prance. As a male runs from his mate, he throws his wings upward until they meet above the back of his body, lowers them, while holding them out from his body, and then brings them toward the sides of his body (Figure 6). The loud Pop sound described earlier accompanies each downward-inward wing motion. The display contains four to five wing-raising cycles, the cycle averaging .43 seconds (SE = .01, range .28 to .89 seconds) between successive wing-up positions. During the last few cycles in the series, the outward-inward motion of the wings occurs twice before the wings are again lifted. In all sequences filmed, the out-in wing motion continued for .33 to .46 seconds after the last wing-up position.

The closed tail is held up and forward over the back (sector A, Figure 6F) during the early cycles and gradually drops (sectors E or F) in the later cycles. This tail position shows off the prominent white tail tips, which are not visible in the normally near-horizontal tail posture.

During the Prance, the postorbital apterium is maximally exposed, the crest position varies from slightly to fully erected, and the contour feathers are sleeked.

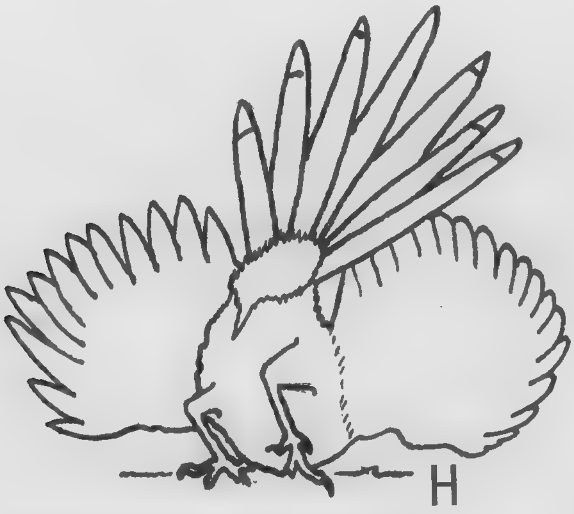


Figure 5. Attack posture with the wings and tail fully fanned.

Tail-wag

Although wild females exhibited Tail-wagging on rare occasions, this is primarily a male display. The display involves a horizontal wagging of the tail while the head is intermittently bowed (sector E or F) and slowly lifted (sector B or C, Figure 7). The head and tail movements are synchronized so that when the head is erect, the tail is closed (Figure 7A); however, as the head bows to the lowest point, the tail fans (Figure 7B) and remains so until after the head is raised again. Only when the tail is fanned are the white tips of the rectrices visible from a frontal view. The angle transected by the wagging tail also varies with the head position, with the widest angle occurring with head erect and the narrowest as the head is raised from the bow (Figures 7A, 7D). A survey of films of 118 Tail-wag cycles – the horizontal movement from one lateral position to the opposite lateral position and back – for three captive and three wild birds revealed that when the head is erect, the tail moves from sectors 2 to 7, 58 percent of the time and from sectors 3 to 6, 42 percent. When the head is bowed I recorded the following tail movements: sectors 2 to 7, 17 percent; sectors 3 to 6, 76 percent; sectors 3 to 5, two percent; and sectors 4 to 5, five percent. During the head lift, the following tail movements were recorded: sectors 3 to 6, 66 percent; sectors 3 to 5, one percent; and sectors 4 to 5, 23 percent.

Tail-wagging occurs more rapidly when the head is bowed and lifted (mean .56 seconds per cycle, SE = .03) than when it is held erect (mean .73 seconds per cycle, SE = .05). Often the Tail-wagging halts or slows appreciably just prior to the head lift (Figure 7B).

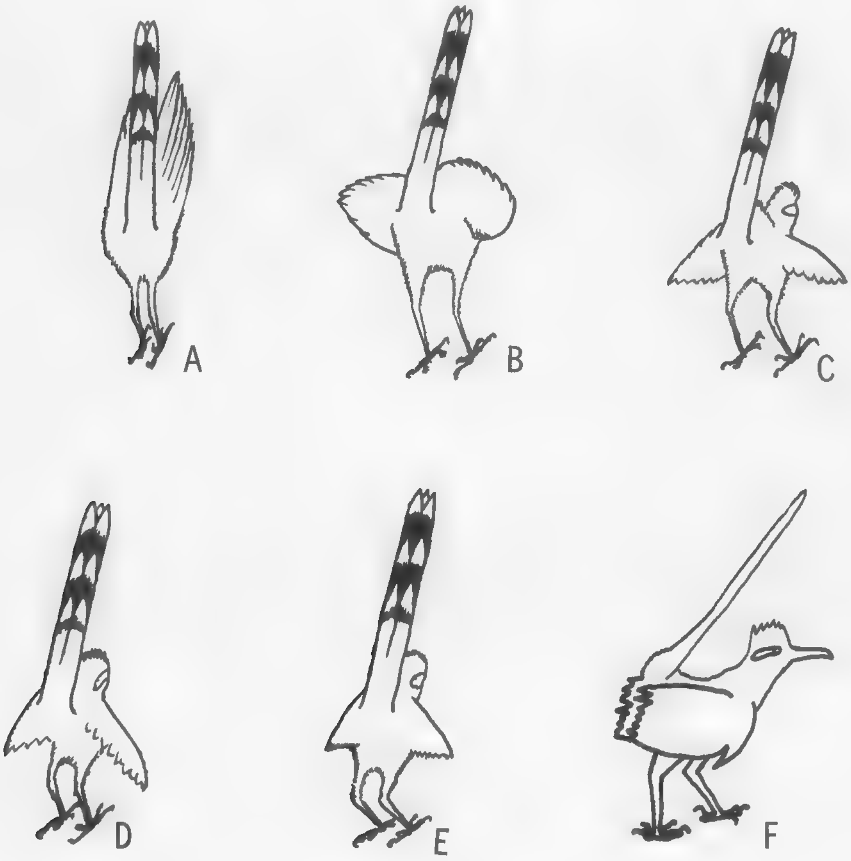


Figure 6. Prance display of the male roadrunner. (A) Male begins running from mate with lifted wings and tail; (B-E) wings are lowered and brought toward the body as he continues running; (F) side view of C.

During the display, the male faces his mate, and as the head bows, the fully exposed postorbital apterium is in her line of vision (Figure 7B). The head-bowing is consistently slower (mean 1.43 seconds per cycle, SE = .20) than the head-lifting (mean 1.01 seconds per cycle, SE = .15). The crest is fully erected throughout the display. The male usually begins the Tail-wag when about 30 meters from the mate, then runs to about three meters and continues the display.

The vocal Whirr display accompanies the Tail-wag, with the *putts* of the call given while the head is erect and the *whirr* produced as the head is lifted from the bow. The bird makes no sound as the head bows.

During the majority of Tail-wag displays, the male holds food or plant material in his bill. This does not appear to affect the form of the display nor the quality of the vocal accompaniment.

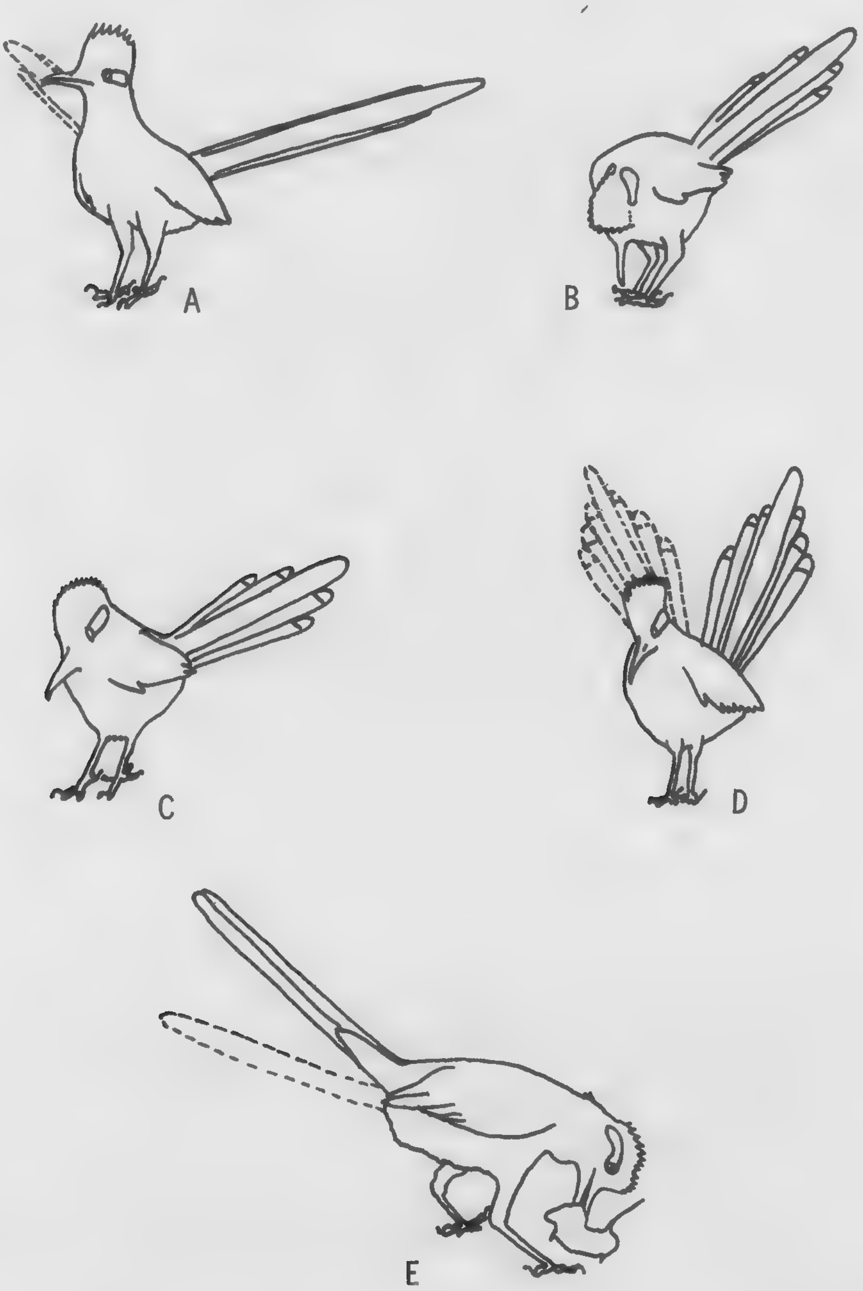


Figure 7. Tail-wag display of the male Roadrunner. (A) Tail-wagging only, showing the lateral extremes of tail motion; (B) tail fanned and stationary as head is bowed; (C) tail fanned as head is lifted from the bow; (D) Tail-wagging continues as the tail is lifted, showing lateral extremes of tail motion; (E) side view of Tail-wagging; the dotted line is the tail position as it is swung back in one cycle of the wag.

Flick-bow

In this display, given by both sexes, the bird bows the head (sector D), emits the Single Coo with a prominent throat bulge, and rapidly flicks the head and tail upward. The crest varies from slightly to moderately erected, the postorbital apterium is partially or fully exposed, and the contour feathers sleeked or relaxed. The display averages 2.6 seconds. The Flick-bow closely resembles the Mutual Flick described later.

Rear Presentation

When the Tail-wagging male is within two to three feet of the female, she consistently orients her body with her posterior toward him. In this position she then performs one of the Flick displays.

Vertical Flick and Side Flick

The female exhibits a rapid flicking of the tail in the presence of the male who is Tail-wagging. Film analyses revealed that two forms of the flick were present: a Vertical Flick that precedes a successful mount by the male; and the Side Flick that precedes an unsuccessful mount by the male when the female moves away. Often I could not distinguish these displays in the field and have referred to them collectively as the Flick display.

In a film sequence of the Vertical Flick, a wild female ran in front of the Tale-wagging male, stopped about 60 cm away, stood with tail slightly fanned (sector F), crest fully ruffled, and postorbital apterium exposed (Figure 8A). As the male began to mount (.39 seconds after she stopped, Figure 8B), her tail moved upward to sector C .22 seconds after his jump began. Simultaneously, her wings flicked down and slightly out. After .22 more seconds, she crouched and lowered her tail (Figure 8C, 8D) until she was in the prone copulation position (.61 seconds after the male landed on her back, Figure 8E). She then slowly sleeked her crest, leaving the postorbital patch fully exposed, raised her head just above horizontal, then lowered it to horizontal. In a film sequence of captive birds, the male did not begin his mount jump until the female had begun the upward flick of the tail.

In the Slide Flick, the female flicked her tightly closed tail initially sideways, then upward, with the crest moderately to fully erected. In a film sequence (Figure 9) a captive female pursued by the male stopped two meters from him, dropped her tail (sector F) and tipped it toward him, then rapidly flicked it upward and away from him. She raised her tail (sector C), providing the male a rear view similar to that presented prior to a successful mounting. She then moved away, lowering her tail (sector D) as the male approached, and erected her crest fully. The tail lift (sector F to C) took .22 seconds. Both sexes exhibit a similar tail flicking throughout the year when approached by another Roadrunner.

Mount

The male mounts from the rear of the female with a jump of one-half to one meter. In a film sequence of mounting, the male began the jump with wings dropped slightly and tail closed, fanning fully both the wings and tail at the summit of the jump (Figure 8B). Rapid wing-flapping and maximum tail fanning accompanied the descent. After landing, the male wing-flapped

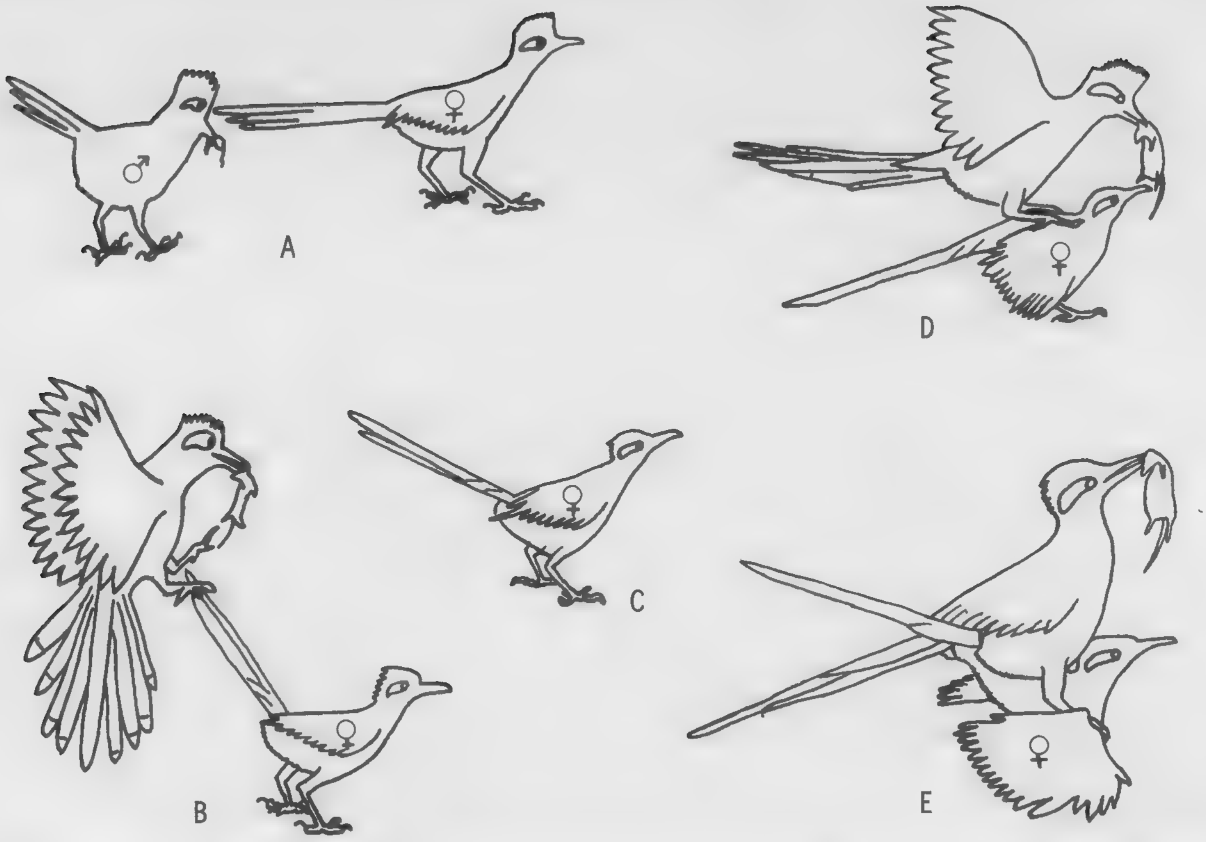


Figure 8. Mounting for copulation. (A) Male exhibits Tail-wag to female; (B) male begins jump as female exhibits Vertical Flick; (C) female lowers her tail and wings as the male (not shown) is above her; (D) male lands on each humeral area of the female; (E) male begins to tread; the upper tail is the female's.

three or four additional times, apparently as a balancing aid (Figure 8D). The crest was fully erected and the postorbital apterium fully exposed during the jump. Numerous observations of unfilmed mounts appeared to be similar to this description.

Copulation

During treading, the female's body is at an angle oblique to the ground, with her breast feathers just touching the substrate and her pelvis elevated. She is supported posteriorly by her legs and anteriorly by her outspread wings (Figures 8E and 10). Her tail is closed and raised (sector D), crest sleeked, and postorbital apterium exposed or partially obscured.

The male treads as he stands erectly on the humeral area of her wings (Figure 8E and 10D). Initially, his tail is horizontal or slightly depressed (sector F, Figure 8E), then raised (sector D or E) and gradually lowered (sector G, Figure 10A). The male fans his tail as he moves it and his pelvis from side to side under the upraised tail of the female (Figure 10B). Initially, the male's crest is fully erected, but it gradually sleeks as treading proceeds. The postorbital area is fully exposed during the sequence. Throughout treading, the captive males continued the Whirr vocalization. I was outside the range of this call while I observed copulation in wild birds.

The vertical displacement of the female's wing with each foot tread of the male was used as a measure of treading rate (Figure 10D). One treading cycle was defined as the rise and fall of the wing to the original position. The treading rate of captive and wild birds averaged .22 seconds per cycle

(SE = .08, n = 152), with rates early in the sequence slower (range: .30 - .34 seconds) than later ones (range: .18 - .23 seconds). Shortly before cloacal contact, the male begins to flap his wings apparently to aid in balance and positioning. The treading rate always increases rapidly near the time of cloacal contact, as the male's tail swings farther to the female's side, rubbing against her cloacal region (Figure 10C).

Simultaneously, the female rises slightly from the substrate and lifts her bill toward the food item (Figure 11). These movements of the female occur even in those situations in which food exchange does not occur, as happens either when the male has no food item (Figure 11H) or when the female holds food intended for the young (Figure 11G). As she grasps the food item, the male's head lowers slightly (Figure 11E). Both birds simultaneously hold the food item for an average of .28 seconds (SE = .05, n = 4) before the male releases it. If the male holds a twig, he drops it early in the treading sequence.

During food exchange, the female's tail is only slightly raised (sector E), the male's more so (sector D). Her postorbital apterium is partially obscured, while his remains fully exposed. The male dismounts .42 seconds (SE = .05, n = 5) after he releases the food item. Upon dismounting, both have tails raised (male in sector E, female in sector B) and crests slightly erected.

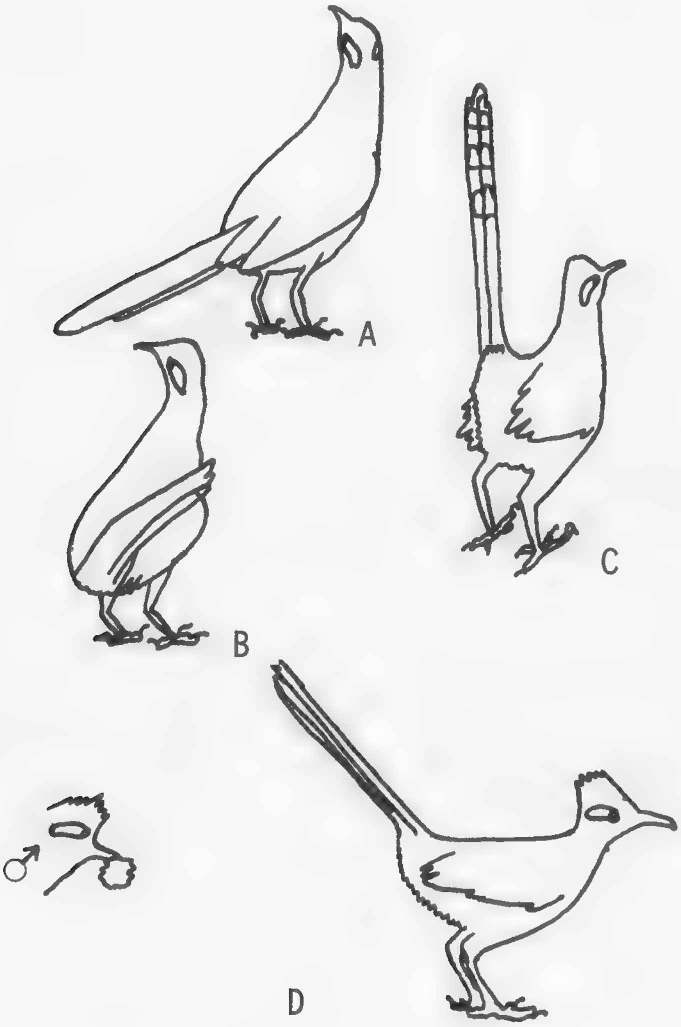


Figure 9. Side Flick of the female as the male Tail-wags. (A) female stops as the male (not shown) pursues and tips her tail toward him; (B) female jerks her tail up and to the side away from the male; (C) female continues raising her tail to an upward, central position; (D) female begins lowering her tail and leaves the area as the male approaches.

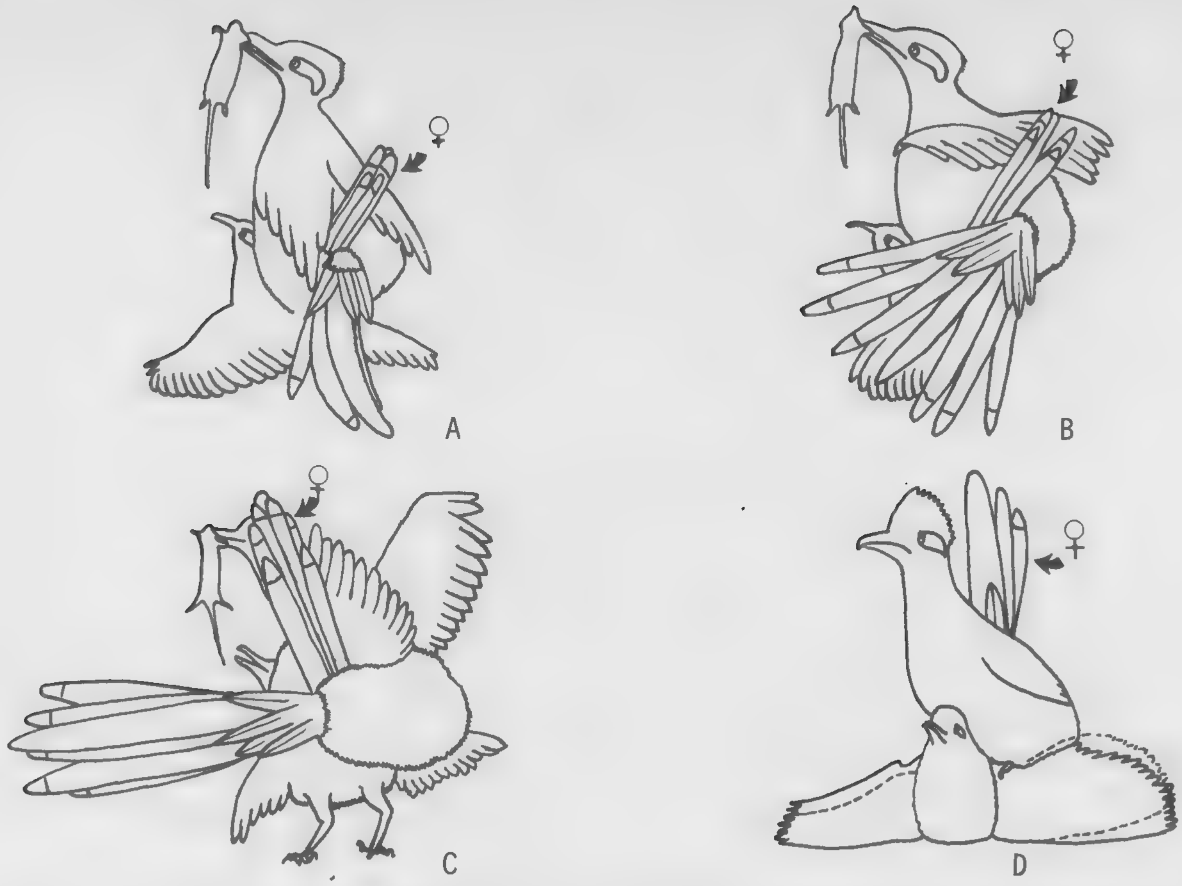


Figure 10. Copulation. (A) Treading early in the sequence; (B) treading just prior to cloacal contact; (C) presumed position during cloacal contact; (D) anterior view of treading; dotted line indicates changes in the female's wing position as he treads.

I did not time entire copulation sequences, but estimates ranged from two to three minutes from the time of mounting to dismounting.

I observed copulation at all times of the day, from shortly after sunrise to just before sunset. About twice as many copulations occurred in the afternoon hours, and the majority of them took place within 20 meters of the nest site.

Mutual Flick

This display follows immediately after the male dismounts and is given by both sexes. The male circles or partially circles the female, who remains on the copulation site and gradually turns her body to face the circling male. The male's tail drops (sector F or G), fans slightly, and turns inward toward the female, while his head points upward (sector A or B, Figure 12A). At intervals in the circling, he stops and presents a side view to the female, bows his head (sector B or C), gives the Single Coo, then rapidly flicks his tail and head upward (tail sector B to E; head sector A to B). He then lowers his tail and either remains stationary and repeats the flick or continues to circle before again stopping and flicking. The wings are dropped below the normal position during the bow, revealing the white wing spots, and lifted above normal with the upward flick (Figures 12B and C). The crest is sleeked or relaxed to slightly erected prior to each flick and becomes slightly or fully erected at the high point of the flick. The postorbital apterium was fully exposed in all birds except a wild female in which the apterium remained partially obscured early in the display. The female exhibits the same flicking display either simultaneously or alternately with the male. Of the four displays analyzed, two of the flicks were given simultaneously and the rest alternately, with four given by the female and

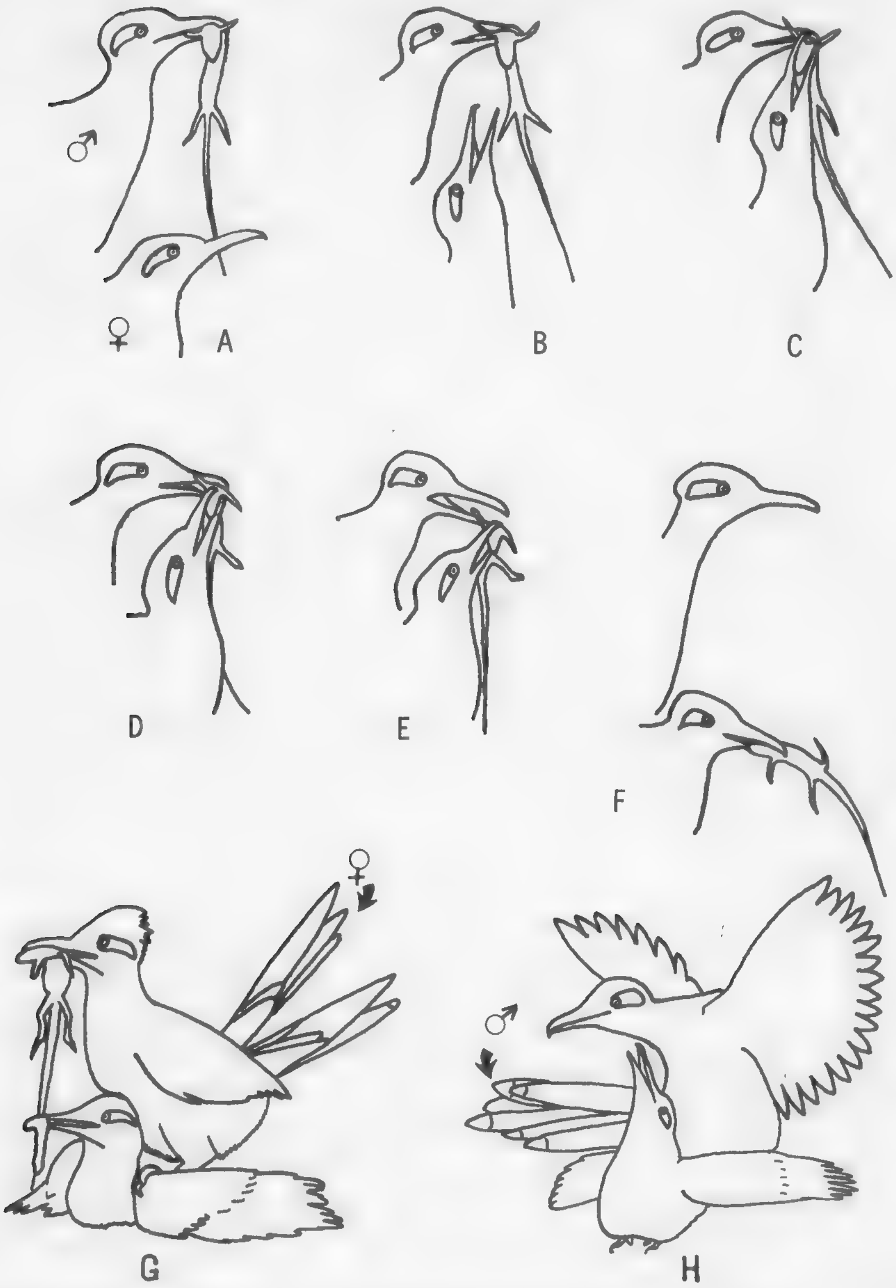


Figure 11. Food exchange during copulation. (A-F) Exchange of lizard; (G) copulation as both sexes hold food intended for nestlings; (H) copulation with no food exchange occurring; note the position of the female's head.

eight by the male. The number of flicks given during one display varied from two to three by the male and one to two by the female. Film analysis revealed a time-motion pattern for this display (Whitson, 1971).

After the display both birds walk away, usually in opposite directions. The female then eats the food, if the display occurs prior to hatching, or feeds it to the young. When both adults held food, each fed the young. After the young had fledged, the female began eating the courtship food occasionally.

Captive Courtship Behavior

All of the behavior patterns described for wild birds occurred in the captive birds and were exhibited to humans, as "sexual imprinting" to humans apparently had occurred during the birds' development. The only male that had a female mate exhibited courthip behavior both to the female and to humans, as did the female.

The captive pair frequently chased one another and humans. The single

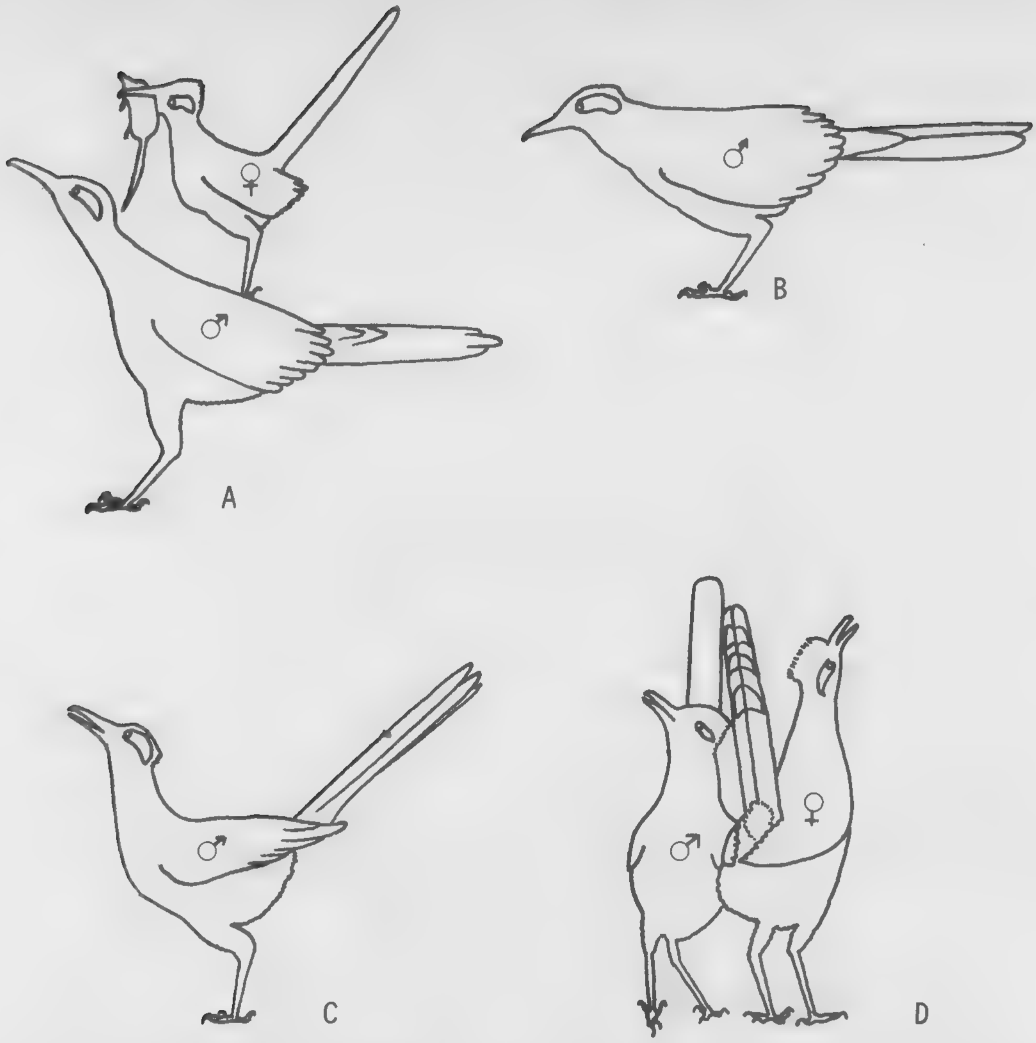


Figure 12. Mutual Flick display. (A) Male circles the female after dismounting; (B) male bows, lowers wings, and gives Single Coo call; (C) male gives an upward head, wing, and tail flick; (D) simultaneous flick by both sexes.

males chased humans, often attacking their feet or legs. Stick-offer was a very frequent male display. Although the female never exhibited this display to humans, she often did so to her mate. However, she emitted the Whine in the presence of a human and subsequently accepted a stick or grass blade offered by a human. The male also accepted sticks from humans.

All captive males frequently performed the Tail-wag when a human approached. The captive female never exhibited Tail-wag. The Tail-wag occurred most frequently at feeding time, when the males used a dead mouse or chick as courtship food. The mated captive male often alternated his Tail-wag between the human and the female. A male often exhibited Tail-wag for an hour or more before consuming the food if a human remained in view. Captive males often mounted a human hand held at ground level.

It was difficult to determine if the female exhibited precopulatory behavior to humans. She frequently exhibited the Side Flick display in the human presence, but her male was also present. She also often exhibited a similar flicking behavior to humans during the nonbreeding season.

The single males exhibited copulatory treading motion on the substrate beside a human or on the human hand. The cloacal contact movements were made by rubbing the cloaca against the human arm, and were followed by the male circling the human in the Mutual Flick display. Films of captives revealed their treading postures, tail movements, and treading rates to be almost identical to those of wild males. Although cloacal contact against the human hand or arm occurred, along with wing-flapping, there was no evidence of ejaculatory fluid. Treading by the male often lasted for ten minutes or more. The male held food items or sticks while treading, but did not release them during the cloacal-contact motions. The food was usually ingested by the male following the Mutual Flick display. When I attempted to remove the food from the male's bill as he treaded, slight force was required, suggesting that he was a passive partner in the food exchange.

Sexual Differences in Courtship

The Coo, Short Coo, Prance, and Food-offer are unique to male Roadrunners, while the Flick is a female display only. The Tail-wag is almost exclusively a male display, while the Bark and Whine are primarily female displays. The other displays are given almost equally by both sexes (Whitson, 1971).

Courtship Patterns

The various courtship behaviors were exhibited as patterns of behavioral interaction between the sexes. Two distinct patterns appeared to be present: pair-bond behavior and copulatory behavior.

Pair-bond Behavior

Pair-bond behavior included interactions between male and female that did not immediately precede copulation and were not exhibited by the pair during the nonbreeding season. Figure 13 summarizes these interactions, indicating those that occurred more frequently. One of the prominent behaviors, especially early in the season, was the Chase. As it was not always possible to identify the sexes, some of the Chases may have been between males. However, the various courtship displays that accompanied the Chase suggested a male-female interaction. The Clack was the most common acoustic signal given by both birds during the Chase. The pursuing male frequently gave the Coo, usually from the top of a shrub or tree. The female often rendered the Bark when she was the pursuing bird. During intervals between Chases, when the birds were in view of one another, the male exhibited Tail-wag, Stick-offer, Growl, Coo, and Whirr, while the female exhibited Flick-bow, Side Flick, Stick-offer, Single Coo, and Whine displays.

Stick-offer was a common pair-bond behavior exhibited about equally by both sexes, especially prior to, and during, nest building. The following behaviors, with their respective percentages of occurrence, accompanied Stick-offer by the male: Tail-wag (66.6 percent), Chase (37.8 percent), Coo (25.2 percent), and Growl (25.2 percent). The female exhibited the following behaviors with Stick-offer: Whine (50.2 percent), Side Flick (37.8 percent), Chase (25.2 percent), and Growl (12.6 percent). Stick-offer by the male most often followed a Whine vocalization by the female, while Stick-offer by the female most often followed Whine, Growl, or Coo by the male.

The Tail-wag, a prominent precopulatory behavior of the male, was often integrated into pair-bond behavior. The male often performed Tail-wag along with Stick-offer, to which the female subsequently exhibited the Whine or Stick-offer. When the male persisted in performing Tail-wag and/or attempted mounting, she gave the Side Flick and left the area, usually followed at a distance

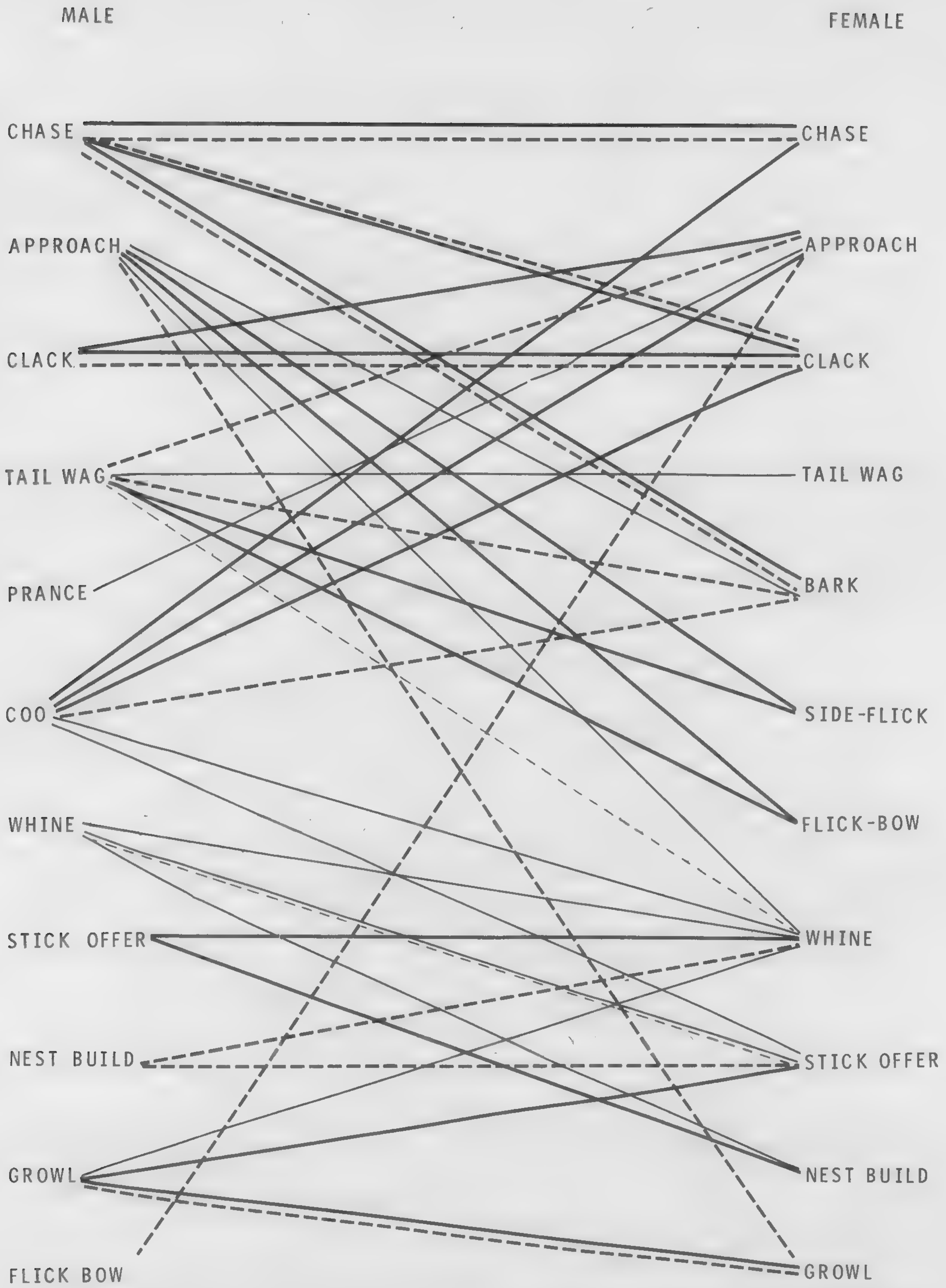


Figure 13. Interactions of Roadrunner courtship during the pair-bond phase of the breeding cycle. The dotted line indicates a female-initiated sequence and the solid line indicates a male-initiated sequence. The thicker lines indicate more frequent interactions.

by the male. While following, he gave the Coo, Growl, and Stick-offer. The female occasionally displayed with the Growl, Whine, and Stick-offer, usually from a bush or tree.

The Prance and associated Pop noise appeared sporadically, performed most often as the male ran from his mate, and was usually followed by her approach.

Copulatory Patterns

Precopulatory behaviors included: Tail-wag, Stick-offer, Food-offer, Coo, Growl, Clack, and Whirr by the male; and Clack, Bark, and Vertical Flick by the female. Figure 14 presents the sequences of behavioral interactions involved in precopulatory and copulatory patterns.

The wild males exhibited the Tail-wag prior to most of the 41 copulations or attempted copulations that I observed. Only males that had been paired for some time and were caring for nestlings did not always give the Tail-wag before copulating. Food-offer or Stick-offer display often accompanied the Tail-wag and copulation. Of the 25 successful copulations observed, 75 percent involved Food-offer. Items offered and their respective numbers included: lizards (12), insects (2), snakes (1), birds (1), plants (1), and unidentified (1). In unsuccessful copulations, items offered were: lizards (4), plants (4), insects (3), and unidentified (3). Lizard species identified at the Texas sites were: *Cophosaurus texanus* (Iguanidae), *Cnemidophorus scalaris* (Teiidae), *Cnemidophorus tigris* (Teiidae), and *Sceloporus* spp. (Iguanidae). A male offering a lizard or bird held it by the anterior portion of the body in the leg or neck area (Figure 11), while a snake was looped several times in the bill. Plant material included small twigs (5 to 8 cm), salt cedar leaves (*Tamarix* spp.), grass blades, and flower buds.

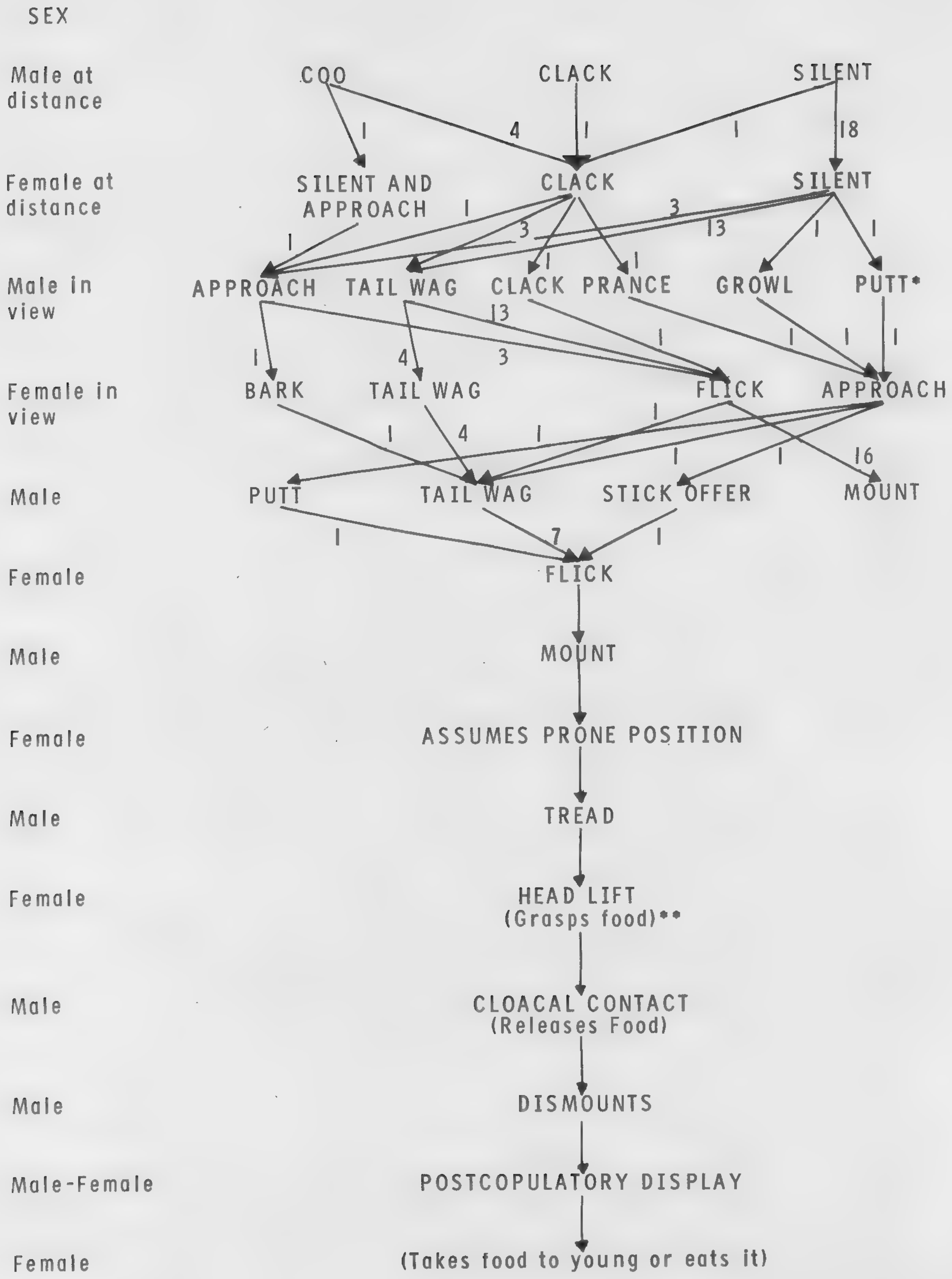
The male consistently gave the Whirr vocalization simultaneously with the Tail-wag as he neared the female for mounting. Other male acoustic signals included the Coo, Growl, and Clack. Females never gave acoustic signals preceding an unsuccessful copulation.

When his copulation attempt was unsuccessful, the male resumed courtship display, pursuing the female, although copulation usually did not occur, at least until later in the day. Immediately after the 17 unsuccessful copulations in the field, I observed the following behaviors and their respective frequencies: males—Tail-wag (13), Chase (6), Growl (3), Coo (2), and Flick (1); females—Flick (6), Stick-offer (4), Whine (2), and Bark (1).

Courtship Patterns and the Breeding Cycle

In some avian species the pair remains together only briefly for courtship and copulation. However, in many species, including the Roadrunner, the pair remains together throughout the breeding cycle, and both parents assume nesting duties. Thus, there is the opportunity for courtship behavior to continue throughout nesting, although its form may change as the breeding cycle progresses. Hence, the description of courtship based on only a part of the breeding cycle may be incomplete.

In this study, I obtained quantitative data on courtship patterns throughout the breeding period, following several pairs through one or two renestings in the same season. The breeding cycle was divided into six periods or phases, which appeared logical for the Roadrunner's nesting behavior but may not necessarily be applicable to that of other avian species. These phases are described below.



*The Putt portion of the Whirr call
**Only when food was involved

Figure 14. Precopulatory and copulatory sequences observed. Numbers indicate the frequency of each behavior observed.

Roadrunner Breeding Phases

(1) *Pair-formation.* – Birds were considered to be in this phase early in the breeding season when only preliminary aspects of courtship, but no copulatory or nest-building behaviors, were exhibited. I observed four breeding pairs and five unidentified single birds in this phase for a total of 43 field-hours.

(2) *Nest-building.* – Nest-site selection and nest-building behaviors occurred during this phase, but no eggs were laid. This phase usually lasted from three to six days, although nest-building activities continued until after the eggs hatched. I observed four wild pairs for 83 hours in this phase.

(3) *Incubation* – This phase begins when the first egg is laid and continues until the time of its hatching. Both birds share equally in the incubation duties. At all nests observed, the male spent the night on the nest, while the female incubated for longer periods during the day. The incubation period is 20 days. I observed four pairs in this phase for 187 hours.

(4) *Early nestling.* – This phase extended from the first hatching until the first nestling was 12 to 13 days old. During this phase at least one parent was always present at the nest, brooding or shading the young, while the other foraged. I observed seven pairs for 221 hours during this phase.

(5) *Late nestling.*—This phase continued until the majority of the nestlings had fledged, which usually occurred at age 19 to 21 days. During this time the adults were seldom at the nest and foraged separately during most of the day. Two pairs began renesting during this phase. I observed six wild pairs in this phase for 211 hours.

(6) *Fledgling.* – This phase extended from the time all the young fledged until they were feeding independently, usually from 30 to 40 days after leaving the nest. During this phase, both parents fed the young and began foraging together. If renesting occurred, it was usually within the week that the first brood had fledged. I observed six wild pairs for 143 hours in this phase.

A summary of the breeding cycle phases is presented in Figure 15, along with the number of copulations occurring in each phase.

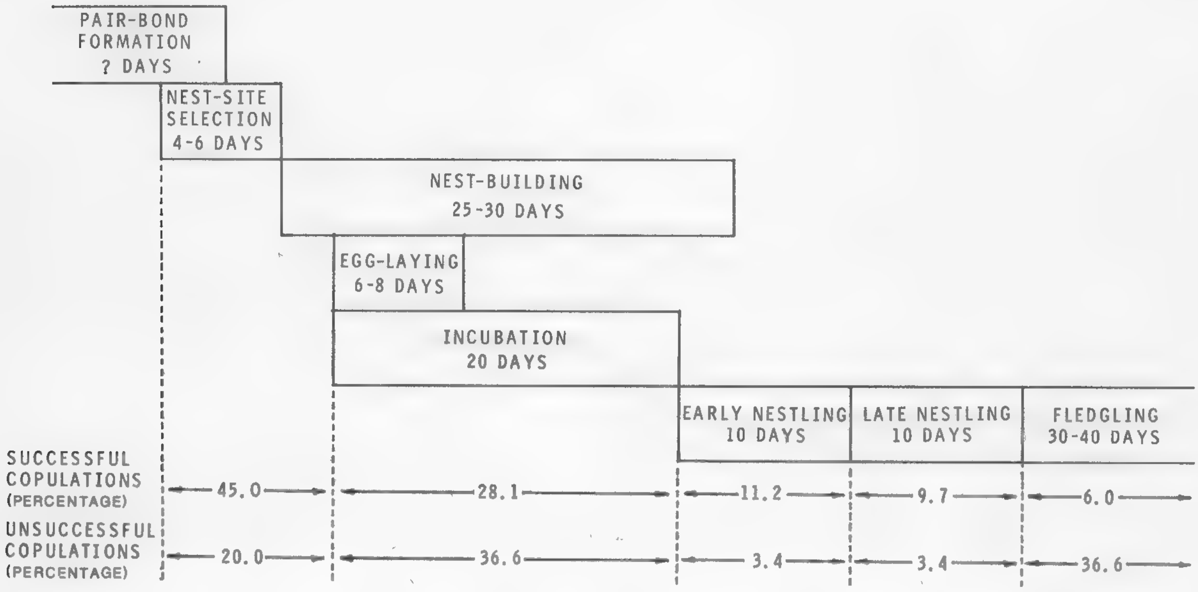


Figure 15. Breeding phases of the Roadrunner, based on a nest with a four-egg clutch. The percentage of successful and unsuccessful copulations during each phase is indicated.

Breeding Phase Patterns

Courtship behavior, its frequency, and the sex performing it during each breeding phase are presented in Table 1. To equalize the disparate observation periods for each phase, I adjusted the frequencies, using the early nesting phase (the one with the most observation hours) as the base line.

The data indicate that wild pairs exhibited courtship behavior throughout the breeding cycle with qualitative, quantitative, and sexual variation of the courtship pattern occurring in different phases. Courtship culminated in copulation in all phases except pair-formation, including those pairs that did not subsequently renest. Pair-bond formation and maintenance behaviors (Chase, Stick-offer, Whine, Growl, Coo, and Bark) occurred most frequently in the pair-formation, nest-building, and fledgling phases. Copulatory behaviors (Tail-wag, Vertical Flick, and Food-offer) appeared most frequently in incubation, nest-building, and fledgling phases. All pair-bond and copulatory behaviors, except the Clack, were at their lowest frequencies during the nestling phases. The Clack also served as an alarm signal and its occurrence may have been in response to dangers near the nest.

During pair-formation, male and female foraged together for all, or a portion, of the day, but usually kept from 5 to 50 meters apart. They often exchanged acoustic signals as they foraged, especially an exchange of Clack or Growl vocalizations. When widely separated, the male gave the Coo and the female the Bark, sometimes singly and sometimes in exchange. While giving the Coo, the male was nearly always in an elevated position. These acoustic signals were also incorporated into the Chase. When the birds were close to one another, one bird commonly gave the Whine, usually followed by a Stick-offer by the other. Occasionally, the male approached the female with the Tail-wag, to which she responded with a Flick-bow or Side Flick, and continued foraging. The pair often roosted in the same, or adjacent, bushes.

I observed mutual Tail-wag displays on several occasions during pair-formation, suggesting that it may be more common for the female to manifest this display at this stage of the breeding cycle. However, the displaying birds were of unknown sex; and since the Tail-wag is also a territorial display, it is likely that some of these observations were territorial encounters between males.

It was during nest-building that the Roadrunner exhibited the highest frequencies of all courtship behaviors, other than the Coo, which was more frequent during pair-formation. Males gave the Coo when separated from their females and as a precopulatory signal. Many of the Barks were given by the female immediately after the occurrence of distant Barks, and usually as she foraged near her mate. The male exhibited no observable response to these Barks. The Growl was given more frequently by the male, although occasionally the pair exchanged Growls as they foraged. Nearly all Stick-offers occurred during this phase, either prior to, or during, nest building. The pair moved into shrubs or trees with the male usually leading. They then sat in, or near, a fork of the plant for a few seconds to a few minutes. The female often emitted the Whine at this time, after which the male descended and returned with a stick. The female either began nest-building with the stick or dropped it, and the pair then descended and climbed again into vegetation.

Many sham nests are started by the Roadrunner before the final selection occurs. The female often builds for only a few minutes with twigs brought by the male, before abandoning the site. When the nest site finally was selected, the female usually built while the male brought the twigs. She often gave a Whine

TABLE 1
Occurrence of Various Courtship Behaviors
of Wild Roadrunners During Each Breeding Phase[1]

Behavior	*Breeding phase*					
	Pair formation	*Nest-building*	*Incubation*	*Early nestling*	*Late nestling*	*Fledgling*
Chase	7.6[2]	3.4 (M,F)[3]				8.0 (M,F)
Clack	38.4	76.8 (M,F)	30.2 (M,F)	53.0 (M,F)	50.9 (M,F)	76.6 (M,F)
Coo	65.3	55.2 (M)	6.5 (M)	7.0 (M)	7.9 (M)	19.9 (M)
Bark	30.7	86.6 (M,F)	20.5 (F)	4.0 (F)	18.1 (M,F)	44.4 (M,F)
Growl	11.5	44.8(M,F)	10.8 (M)	4.0 (M)	4.9 (M)	17.6 (M)
Whine	23.0	47.4 (F)	3.2 (M,F)	1.0 (F)	1.6 (F)	6.0 (M,F)
Tail-wag	6.8	39.8 (M,F)	8.6 (M)	4.0 (M)	4.0 (M)	22.2 (M)
Flick	3.2	13.3 (F)	12.3 (F)	2.0 (F)	3.6 (F)	10.9 (F)
Flick-bow	1.5	6.9 (M,F)	1.1 (F)	1.0 (F)		1.6 (F)
Stick-offer	4.2	41.6 (M,F)	1.1 (M,F)		1.6 (M,F)	6.4 (M,F)
Food-offer		15.9 (M)	9.6 (M)	4.0 (M)	3.6 (M)	4.4 (M)
Prance			1.1 (M)	2.0 (M)	2.6 (M)	2.8 (M)
Copulation		11.9	7.5	3.0	2.6	1.6
Copulation attempt		6.0	10.8	1.0	1.0	10.8

[1] Values represent the number of times each behavior was observed and are adjusted to equal observation times.

[2] Sexes unknown in this column

[3] M, known males that performed the behavior; F, known females that performed the behavior.

while he was on the ground or as he ascended the nest plant. Occasionally she joined the male in gathering twigs. It was not uncommon for the male to Whine from the ground or a bush and for the female to bring a stick to him, although this never occurred after the final nest site was selected. Copulation occurred most frequently during the nest-building stage, usually near the nest site.

During incubation the pair exhibited the same diversity of behaviors as during the nest-building stage, although less frequently. The Clack and the Bark were the most common acoustic signals, usually given by the bird on or near the nest. Many of the Barks were given by the incubating female in response to distant Barks. The male did not respond to Barks while incubating, but gave a Coo in response to distant Coos while sitting. The incubating bird and its nearby mate often exchanged Clacks. Other Clacks were given in response to disturbances at the nest. The Growl was most often given by the male as he foraged near the nest. The male rendered the Coo as he approached the nest, usually prior to copulation. Copulation was only slightly less frequent than during nest-building and always occurred at the nest site or within five meters of it. Prior to most copulations, the male gave the Coo or Clack as he approached the incubating female, but while out of her view. He began the Tail-wag as he reached the nest tree. The female either responded with the Clack or was silent, then immediately flew down and landed near the male. Both sexes continued to add lining material to the nest at this time.

Courtship behaviors reached their lowest frequencies during nestling phases. The most frequent vocalization at this time was the Clack, most often given when there were disturbances near the nest, such as another bird landing in the plant containing the nest. The brooding bird and its nearby mate also exchanged

Clacks. Copulation continued to occur, although at a lower frequency. The female rendered the Bark in response to distant Barks by other Roadrunners, and as she stood over the young prior to feeding them. The Whine and Stick-offer occurred in two females already engaged in nest construction just prior to the fledging of their first broods.

During the fledgling phase, there was a resurgence of courtship behavior and copulation. Several of the pairs under observation engaged in fledgling care and nest-building simultaneously. Generally, those courtship behaviors that occurred around the new nest were included in the data for the nest-building phase. This increased courtship behavior definitely correlated with renesting in two of the pairs, and possibly in several of the others for which follow-up was not possible. The male usually courted either with no food or with a stick. Also, the highest frequency of unsuccessful copulations occurred at this time, primarily in those pairs that I am not certain renested. The majority of unsuccessful copulations occurred in a pair which evidenced no nest-building behavior. Only during this phase did a male exhibit the Bark. These were given in response to distant Barks as he was with the fledglings, or upon the appearance of a strange Roadrunner in the area of the fledglings, often followed by an attack and chase to drive off the stranger. No other wild or captive males were ever heard to exhibit the Bark.

The Chase during this phase, in contrast to that of pair-formation, usually included several attempted copulations. The Whine was given during nest-building by the females and by the males as they carried sticks to her. The increase in Coo was also associated with chasing strangers or fledglings from the first brood away from the area of the new fledglings.

Courtship Patterns in Captive Birds

Even though there was not a complete breeding cycle exhibited in captivity, these observations are of value in supplementing those of the wild birds, for I had more opportunities to observe early pair-formation in captive than in wild birds. Also, I knew the ages of the birds and therefore gained some insight into the breeding behaviors in first-year birds.

The captive pair exhibited breeding cycle distortions perhaps related to the effects of hand-rearing, inappropriate environmental stimulation, and their age. For instance, nest-building, usually accomplished in a few days by wild pairs, extended over 26 days in these first-year birds. Incubation was intermittent and no eggs hatched, although one was fertile. Many attempts at nest construction occurred during the incubation period.

During the breeding phases of the captive pair, courtship patterns occurred that were similar to those exhibited by the wild birds. Similar to wild birds, acoustic signals were more prominent early in the season. The captive male exhibited the Short Coo, simultaneously with Tail-wag, both to the captive female and to humans, although this call was never given by wild paired males. Perhaps this is only given in the wild by inexperienced, first-year birds. The captive male gave the Whine much more frequently than wild males, while the captive female rendered the Flick-bow more frequently than the wild females. Early in the season the female was more often the aggressor in the Chase; later this situation was reversed. The Chase almost disappeared by the incubation phase. The Prance of the male was at its highest frequency early in pair-formation, although it never was observed during pair-formation in the wild. The Prance appeared again during the incubation phase only when the pair had ceased incubating prior to

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Greater Roadrunner, *Geococcyx californianus.* Painting by Albert E. Gilbert.

Albert Earl Gilbert
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a new nest-building attempt. Its high frequency in single males correlated with increased Tail-wag displays to humans.

The single males also exhibited variation in their courtship pattern throughout the season. Coo, Stick-offer, and Prance preceded any copulatory behavior by several weeks. One captive exhibited aggressive behavior toward humans, also. The Tail-wag preceded any attempts to mount the human hand by several days, while the cloacal contact motions and Mutual Flick display were not exhibited until several days later. Although they exhibited no nest-building activity in captivity, two of the captive males built nests alone after their release into the wild during the breeding season.

Courtship Exhibited by Juveniles

Juveniles of some birds have been observed to exhibit components of courtship behavior that are not normally seen in their entirety or in proper context until sexual maturity. The most common example is the subsong of juvenile male passerines (Lanyon, 1960). The hand-reared and wild young observed in this study provided an opportunity to note the ontogeny of courtship behaviors in the Roadrunner (Table 2).

Ten wild young were observed as nestlings and fledglings: three from about 30 to 91 days of age; four from 1 to 23 days of age; and three from 1 to 38 days of age. The wild young normally fledged when 19 to 21 days old and remained with their parents until about 50 to 60 days old.

I observed seven captive birds from nestlings to adults. One young was hatched in captivity and reared in isolation from other Roadrunners.

The wild young exhibited typical Roadrunner courtship behaviors, with the exception of the Prance, copulatory behavior, and Mutual Flick display (Table 2). The Tail-wag consisted only of tail-wagging and head bowing components, without the accompanying Whirr. During the Whine, often only the head motions occurred without any accompanying sound. The Tail-wag, Flick-bow, Side Flick, and Stick-offer were exhibited to the parent and by several young to a captive adult male that was released into the wild. Juveniles alone and unattended by a parent gave the Coo, Bark, and Clack. Juveniles exhibited the Clack and Growl in response to the same signal by a nearby parent. Intersibling signals were limited to the Growl, Clack, and Stick-offer. The Flick and Whine appeared following an attack by a parent or when the threat of parental attack was imminent. On one occasion Stick-offer and Tail-wag were exhibited by a juvenile to an adult. The Clack was first heard when the young were left alone in the nest. Erection of the crest and exposure of the postorbital apterium first occurred, along with the Clack, when a new stimulus appeared in the nest environment, such as an insect flying by or another bird landing in the nest bush.

The major difference noted between the captive and wild young was the relatively fewer acoustic signals exhibited by the captives (Table 2). The captives rendered only the Clack and the Whine. The isolated bird exhibited the Bark, although on one occasion only. The Clack, erection of the crest, and exposure of the postorbital apterium appeared when the juvenile was placed in a new situation or confronted with a new stimulus. The Tail-wag consisted only of the tail-wagging component, appeared only during food-begging, and was accompanied by a begging call and wing-flapping. The Flick and Stick-offer were oriented to humans and to siblings. Even though never attacked by humans, the captives exhibited the Whine and Flick to humans as had wild juveniles when attacked by their parents.

The isolated juvenile was the only young Roadrunner observed to exhibit cloacal contact motions and Mutual Flick display. This was elicited by human application of slight rubbing motions on the cloaca of the bird. The other captives also may have exhibited this behavior had a similar stimulus been applied.

The Coo as a Releaser of Courtship Behavior

To elucidate the role of this signal in stimulating courtship as the breeding season changed, I presented a tape with the Coo vocalization or imitated the Coo to wild pairs in their breeding territories throughout the season and observed their responses. Roadrunners that were encountered early in the breeding season were also tested and included in the data for the pair-formation phase. I also tested captive birds with the human out of sight of the birds.

I found that the Coo was capable of eliciting a variety of male and female courtship behaviors (Table 3). No differences in response to the tape or to the human imitation were noted. Most noticeable was the diversity of responses elicited during nest-building, including displays involving both pair-bonding and copulation. The males exhibited responses more frequently throughout all the breeding phases, whereas the females rarely or never responded during incubation or nestling phases. The Preen, not previously described, was a rapid breast, or flank, preening.

Comparing the responses to the experimental tape with naturally occurring behaviors (Table 1) for these same birds, I found that the Bark and Whine, primarily female signals, were exhibited with low frequency during incubation and nestling stages in both natural and experimental situations. On the other hand, the male's Coo was infrequent during incubation and nestling phases,

TABLE 2

Appearance of Courtship Behavior in Juvenile Roadrunners

Behavior	*Wild young*	*Number of birds observed*	*Captive young*	*Number of birds observed*	*Isolated juvenile*
Clack	8[1]	10	8[1]	6	8[1]
Coo	37	2			
Bark	35	2			33
Growl	34	3			
Single Coo	70	2			
Whine	35	5	22	6	23
Tail-wag	35	2	30	4	
Flick	34	2	32	6	20
Flick-bow	70	2			
Stick-offer	23	6	23	6	22
Crest movement	12	10	12	7	12
Postorbital apterium exposure	12	10	12	7	12
Copulatory motions					1
Postcopulatory display					1
Number of birds observed		10		7	1

[1] Numbers in these columns indicate the age in days of the bird when the behavior was first exhibited. Ages were averaged when several young exhibited the behavior.

but was relatively frequent in response to the Coo signal during these same phases.

The captive pair exhibited a similar response pattern to the Coo tape, except that the Flick, Preen, Tail-wag, Food-offer, and Prance were not exhibited. However, the captive, but not the wild, pair exhibited the Growl.

Visual Stimuli of Courtship Behavior

As the Roadrunner lacks obvious sexual dimorphism, I hypothesized that the male uses behavioral cues to identify the female and vice versa. I conducted preliminary tests of obvious behavioral differences between the sexes to determine their stimulus value. The copulatory posture of the female and the Tail-wag of the male were simulated by models and used in the tests. The female model was a taxidermically prepared female skin mounted in the female copulatory position. The male model was mechanized to perform the characteristic tail and head movements of the Tail-wag and was prepared from balsa wood that was carved and painted to resemble a Roadrunner. The colors of the postorbital apterium were duplicated as closely as possible; however, as the sexual color difference in this area was not known at the time (Folse, 1974), I painted both models using a wild male as a model. A male Roadrunner skin, mounted in a non-courting posture with wings held out and fanned slightly and tail raised was used as a control model. (See Whitson, 1971 for a more detailed description of these models).

Each of the models was presented to (1) seven wild pairs in their breeding territory during each breeding phase other than pair-formation, (2) one pair during pair-formation, and (3) the captive pair. Each model was presented alone, and later in combination with the experimental tape. The responses were compared with those exhibited by these same pairs to the Coo tape alone (Table 3). I frequently filmed the responses for detailed analysis.

I recorded no differences between responses to the various models. No males or females exhibited courtship behavior to the model presented alone; but males gave a variety of displays (Coo, Short Coo, Tail-wag, Prance, and Clack) when a model was presented in combination with the Coo tape. However, a greater number of males responded to the Coo tape alone than to the combined model and Coo. No males attempted copulation with a model. A few females exhibited courtship behavior (Whine, Stick-offer, Bark, Clack, and Flick) to the Coo tape alone and to the model-Coo. In contrast to the males' responses, females showed these displays more frequently in the model-Coo situation than when presented with the Coo tape alone.

Both sexes exhibited several responses to the model that were not courtship and appeared to be similar to displacement activities described for other birds. The Bill-wipe was a rapid sidewise bill-wiping on the substrate similar to that exhibited after feeding. The Preen was a rapid, jerky preening of the breast or flank, and the Head-scratch was a rapid scratching of the head with the foot.

Other behaviors exhibited to the model were the Crouch, the Circle, and the Attack. In the Crouch, the female lowered the body with sleeked feathers to near ground level in the presence of the model alone. The Circle, given frequently by both sexes, involved circling of the model with the tail lowered and fanned; periodically the tail was tipped sideways and upward, presenting a view of the white tips of the rectrices. In Attack, the bird faced the model with wings drooped and tail forward (sector A) and ran at the model while fully fanning the tail and wings. The bird jabbed at the model with the bill, often

TABLE 3
Responses of Wild Roadrunners
to the Experimental Tape of the Coo Vocalization
During Each Breeding Phase

Response	*Breeding phase*					
	Pair formation	*Nest-building*	*Incubation*	*Early nestling*	*Late nestling*	*Fledgling*
Approach[1]	12.1[2], [3], [4]	33.3 (M,F)[3], [4]				16.7 (M,F)
Chase	9.1	4.7 (M)				
Stick-offer		4.7 (F)				
Whine	15.1	14.2 (F)				
Flick			12.5 (F)			
Bark	36.3	28.5 (F)				7.6 (M,F)
Preen		4.7 (F)	12.5 (M)		18.1 (M,F)	
Prance	12.1	4.7 (M)	25.0 (M)	9.1 (M)	45.4 (M)	34.6 (M)
Clack	15.1	23.8 (M,F)	12.5 (M)	9.1 (M)	45.4 (M)	34.6 (M,F)
Coo	21.2	42.8 (M)	37.5 (M)	54.6 (M)	90.9 (M)	84.6 (M)
Tail-wag		4.7 (M)	25.0 (M)	9.1 (M)	36.2 (M(	15.2 (M)
Food presentation					9.1 (M)	3.8 (M)
Number of tests	33	21	8	11	11	26
Number of birds tested	31	10	8	10	8	8

[1] Approached the sound source only and gave no further response.

[2] Sexes not determined in this column.

[3] Values are percentages of the birds tested that gave that response.

[4] M, known males that performed the behavior; F, known females that performed the behavior.

tearing out feathers. Males attacked the model alone, while females attacked both model and model-Coo. The male often alternated Tail-wag and Attack in the model-Coo experiment, accompanied by Bill-wipe, Preen, Head-scratch, Coo, and Short Coo.

The captive pair did not exhibit courtship behavior to any of the models nor to the model-tape experiment, although they did exhibit Circle, Crouch, Preen, and Attack.

Discussion

Summaries of the major male and female courtship behaviors are presented in Tables 4 and 5. Functions for each behavior are suggested from various lines of observational evidence and from the results of the model-tape and tape experiments.

Various functions have been postulated for the elaborate and lengthy preliminary courtship exhibited by many species. The long courtship period that facilitates pair-bond formation and maintenance is most common in bird species that stay together throughout the breeding season. That pair-bond formation and maintenance are primary functions of the various pair-bond behaviors described for the Roadrunner is supported by the observations that the Roadrunner pair (1) remains together throughout the season, (2) is often double-brooded, and (3) exhibits a resurgence of these behaviors prior to renesting. A long preliminary courtship also may promote sexual and individual recognition in non-dimorphic species such as the Roadrunner. The pair may also be establishing the nesting territory as they forage together in the pair-formation stage. In areas where *G. californianus* and the Lesser Roadrunner *(G. velox)* are sympatric, the differences in pair-bond behaviors between the two may promote species distinctiveness. Marler and Hamilton (1966) postulate that an initial species-specific courtship insures reproductive isolation of the species.

A primary function of the visual and acoustic displays that characterize precopulatory behaviors of many avian species is the synchronization of the reproductive physiology and behavior of the pair (Marler and Hamilton, 1966). The male's display promotes receptivity of the female, while the female's display indicates her readiness for copulation.

Avian courtship behaviors have been observed to reflect not only sexual tendencies, but also tendencies to attack and to escape from the mate or potential mate (Hinde, 1953). Thus, both pair-bond and precopulatory behavior serve another function by reducing normal intraspecific hostile behavior (Dilger, 1956).

The derivation of most avian courtship displays is assumed to rest with these sexual, aggressive, and escape tendencies (Bastock, 1967). Ritualization of intention movements (incipient or incomplete movements) of aggression and escape is the source of many courtship displays (Daanje, 1950). Components of the Roadrunner courtship behaviors that suggest agonistic derivation are the vertical, fanned tail position of the Tail-wag, erection of the crest, and Chase. Fleeing tendencies are evident in the Mutual Flick display, Flick, Flick-bow, and Prance.

Other suggested sources of courtship displays include parental behavior, nest-building movements, infantile behavior, and alerting postures (Andrew, 1961). The head movements of the Stick-offer and Whine resemble nest-building behavior, while Food-offer suggests parental behavior. Several behaviors could have infantile origins. The Chase resembles play in young Roadrunners; the Tail-wag resembles the tail movement during begging by juveniles; and the Whine and Flick-bow appear in the young as appeasement behaviors to the parent.

The functions and derivations of the various courtship displays of the Roadrunner are discussed more thoroughly in the following paragraphs.

Crest Erection and Postorbital Apterium

Since Roadrunners prominently exhibit the brightly colored postorbital apterium, the latter probably plays a role in species recognition. The prominent display of such brightly colored species-specific structures is common in avian courtship (Tinbergen, 1948). This same area is red rather than orange in *G. velox,* and may possibly have developed as a reproductive isolating mechanism. The slight sexual difference in coloration of the apterium (Folse, 1974) may also be a cue for sex recognition. The greater frequency with which the male displayed the bare area may also indicate sex.

Crest erection in many birds, including the Roadrunner (Figure 2), indicates agonistic behavior and serves to increase the apparent size of the bird during attack or threat (Dilger, 1956). Morris (1956) suggests that crest erection is derived from a ritualization of an autonomic pilomotor response in situations involving thwarting behavior. This usually results in the erection of contour feathers during courtship, but ritualization may have restricted piloerection to special areas of the body, enlargement of these particular feathers, and the

TABLE 4
Summary of Male Roadrunner Courtship Behavior

Behavior	*Recipient of behavior*	*Associated behavior*[1]	*Associated call*[2]	*Female's prior behavior*	*Female's subsequent behavior*	*Breeding cycle occurrence*[3]	*Probable major functions*	*Other functions or occurrences*
Chase	Female	Tail-wag, Stick-offer	Growl, Coo, Clack	Approach, Bark	Run, Clack, Bark	Pair-formation, fledgling care	Form pair-bond; sex recognition	Play in young birds; territoriality
Stick-offer	Female	Tail-wag, Chase	Coo, Growl	Whine, Stick-offer, Flick-bow	Whine, Nest-building	Nest-building	Form pair-bond; stimulate nest-building	Nest-building
Prance	Female, Coo tape, model-tape	Tail-wag	Pop[4], Coo	Approach	Approach	Pair-formation	Attract female; sex recognition	Startle predator; territoriality
Tail-wag	Female, Coo tape, model-tape	Stick-offer, Food-offer, Chase, Copulation	Whirr[4], Coo, Growl, Short Coo	Clack, Bark, Whine	Vertical Flick, Flick-bow, Side Flick, Stick-offer, Whine	Nest-building, fledgling care	Form pair-bond; sex recognition; stimulate female for copulation	Territoriality
Food-offer	Female, Coo tape, model-tape	Tail-wag	Whirr, Coo	Clack, Bark, Whine	Vertical Flick, Side Flick, Flick-bow	Nest-building, incubation	Promote female receptivity	Provide nourishment for egg-laying; time breeding to food supply
Flick-bow	Female		Single Coo[4]	Approach, Bark		Nest-building	Reduce aggression when birds are close	Given by young when approached by parent

[1] Indicates a behavior exhibited by the male either simultaneously or immediately before or after the primary behavior.

[2] Indicates the acoustic signal accompanying the behavior.

[3] Indicates when in the breeding cycle the behavior was most frequent, although most signals occurred throughout the cycle.

[4] Indicates that the acoustic signal always occurred with that behavior.

TABLE 5
Summary of Female Roadrunner Courtship Behavior

Behavior	*Recipient of behavior*	*Associated behavior*[1]	*Associated call*[2]	*Male's prior behavior*	*Male's subquent behavior*	*Breeding cycle occurrence*[3]	*Probable functions*	*Other functions or occurrences*
Chase	Male	Stick-offer	Clack, Bark	Coo, Chase	Run, Chase	Pair-formation	Form pair-bond; sex recognition	Play in young birds; territoriality
Stick-offer	Male	Chase	Whine, Growl	Growl, Coo, Whine	Stick-offer, Whine, approach	Nest-building	Form pair-bond; stimulate male to nest-build	Nest-building
Vertical Flick	Male	Copulation, rear presentation		Coo, Tail-wag, Growl, Food-offer, Whirr, approach	Mount to copulate	Nest-building, incubation, fledgling	Indication of sexual receptivity	
Side Flick	Male, model-tape, Coo tape	Avoids male		Same as for Vertical Flick	Unsuccessful mount	All stages	Indication of unreceptive female	
Flick-bow	Male		Single Coo[4]	Approach, Tail-wag, Whirr		Pair-formation, nest-building	Reduce aggression when birds are close	Given by young when approached by parent
Tail-wag[5]	Male	Copulation, nest-building		Tail-wag	Tail-wag, mount	Nest-building	Stimulate nest-building; indicate sexual receptivity	

[1] Indicates a behavior exhibited by the female either simultaneously or immediately before or after the primary behavior.

[2] Indicates the acoustic signal accompanying the behavior.

[3] Indicates in which phase of the breeding cycle the behavior was most frequent, although most behaviors occurred throughout the cycle.

[4] Indicates that the acoustic signal always occurred with that behavior.

[5] Only rarely observed in the wild, and never in captivity. The associated Head-bow and sound of the male Tail-wag did not occur.

addition of color to the erected area. Such ritualization seems to have occurred in the Roadrunner's crest, correlated with the absence of contour feather ruffling during courtship.

The orange postorbital apterium adjacent to the crest is not dependent on crest erection for exposure, although the two usually occur simultaneously during Roadrunner displays. In addition, the conspicuous head bowing movements of the Tail-wag display in the male serve to show off the top of the crest and the orange apterium to the female.

Friedmann (1933) reports crest erection during courtship by the Striped Cuckoo, *Tapera naevia.*

Stick-offer

Stick-offer appeared to stimulate and synchronize the nest-building efforts of the pair, and was most prominent during this activity. There was a resurgence of Stick-offer in the courtship of wild and captive birds when new nests were being built during the season. In the wild, Stick-offer during the incubation period may have been related to the fact that construction of the nest lining was not complete until after the eggs hatched. The appearance of Stick-offer long before nest-building suggests its role in pair-bond formation.

When food was not available, captive males occasionally gave the Stick-offer in place of Food-offer. Captive males that exhibited Tail-wag without food did not approach a human until they had found a stick to carry. Wild males similarly substituted a stick for food during Tail-wag. The presence of any object in the bill probably reduces aggression in the mate.

Stick-offer has been reported in the Yellow-billed Cuckoo, *Coccyzus americanus,* as a copulatory behavior (Hendricks, 1975). It is a common avian courtship display (Tinbergen, 1952).

Chase

The Chase was one of the earliest interactions between the sexes and recurred prior to renesting, suggesting a pair-bond function.

The sexual chase is a common behavior in avian courtship, although it is usually aerial. Sexual chases are thought to be an expression of sexual motivation that would otherwise be directed to copulation, or an expression of aggression (Marler, 1956). During the fledgling stage, the Chase by the male correlated with the highest frequency of refusals to copulate by the female for any breeding phase.

Prance

A paired wild male rarely exhibited the Prance and did so only in the presence of his mate. However, the Prance was a relatively frequent response to the taped Coo vocalization, occurring in association with the Coo and Tail-wag responses. It also was a common behavior of captive males early in the season and recurred in the paired male prior to each renesting. These observations suggest that the Prance plays a role in early pair-formation. The loudness of the Pop sound and the prominent wing movements suggest it serves primarily to attract the female.

The components of the Prance appear to be derived from a tendency to flee. A vertical tail position is considered to be derived from the flight intention movement (Daanje, 1950). Also, the displaying bird always ran from the mate or sound source.

During the Prance and Flick displays, the tail is not fanned, in contrast to other displays in which the tail is also held in the vertical position (Tail-wag and attack positions). This suggests that raising the tail may serve to display the white tips of the rectrices, for during Tail-wag the displaying bird faces the partner, and in this position the spots are not visible unless the tail is fanned. However, during the Prance and Flick displays, with the rear view presented to the partner, the white tips of the rectrices stand out more than when the tail is fanned.

A similar display with accompanying noise has been observed in the male Spruce Grouse, *Canachites canadensis,* where it probably functions as a territorial behavior (MacDonald, 1968). Some species of hummingbirds exhibit an aerial wing popping thought to attract females (Busnel, 1963).

Tail-wag

This display usually preceded copulation, suggesting its function in promoting female receptivity. Also, it was the prominent display of the male as he followed the female after she refused to copulate. That the Tail-wag model did not induce female receptivity could be accounted for by the fact that the experiment involved only paired females, and they may have recognized and responded only to their males.

The fanned tail in the vertical, or near vertical, position during Tail-wag closely resembled the attack posture. This behavior resulted in the bird appearing larger than normal, a characteristic of agonistic displays.

The head bowing component of the Tail-wag resembled the head bowing reported for passerine courtship, where it is thought to be derived from the placement movements of nest-building or feeding the young (Andrew, 1961). However, the Roadrunner head bowing does not resemble any of its nest-building or feeding movements. Only in the Coo and Short Coo is the head also bowed; these movements possibly share a common origin with the head bowing of the Tail-wag. One of the primary functions of head bowing may be to reveal the exposed postorbital apterium.

A similar display involving tail-wagging, crest erection, and conspicuous wing movements, but lacking the head bowing, was described for the Striped Cuckoo by Friedmann (1933). The courting male Inca Dove, *Scardafella inca,* which also possesses white-tipped rectrices, displays with tail raised and fanned (Johnston, 1960).

Female Precopulatory Behavior

As the female consistently exhibited Rear Presentation and Vertical Flick prior to successful copulation, these behaviors undoubtedly indicate her sexual receptivity. That males could not be stimulated to mount the stationary female model, even though they exhibited precopulatory displays, suggests that the cue for female receptivity was absent and was quite likely the Rear Presentation or Vertical Flick.

The Side Flick exhibited by unreceptive females possibly indicated their breeding state to the male, for the male rarely attempted mounting in this case, although he continued to display with the Tail-wag.

Hamilton and Hamilton (1965) reported a precopulatory display of the female Yellow-billed Cuckoo similar to an exaggerated flight intention movement with the tail straight up. I observed a rapid series of tail flicks by a female Yellow-billed Cuckoo preceding copulation.

Flick-bow

Both sexes rendered a behavior similar to the Flick-bow throughout the year, usually as another Roadrunner approached or when encountering a strange object. Young birds also gave the behavior when approached by an adult. The situations in which flicking occurred during the nonbreeding season suggested an appeasement function designed to prevent attack by reducing aggression in the approaching bird. The tail and wing flick components were similar to those exhibited by many species in similar situations and are thought to be derived from flight intention movements (Andrew, 1961). The Vertical Flick, Side Flick, the Flick-bow, and the flick component of the Mutual Flick are all similar in form and all occur in situations where a reduction of aggression in the partner might be warranted, such as very close proximity of members of the pair.

Mutual Flick

Postcopulatory displays are reported for relatively few avian species, being most widespread in the Anseriformes (Johnsgard, 1965). The adaptive significance of postcopulatory displays is not clearly understood, since selection pressures are usually exerted on behaviors that precede copulation. Maintenance of the pair-bond and prevention of aggression between the pair following copulation are proposed functions. Postcopulatory displays occur more commonly in species, such as the Roadrunner, that maintain a pair-bond and where both parents share nesting duties.

Food-offer

Courtship feeding by the male Roadrunner was reported by Rand (1941) and Calder (1967). Both authors described food exchange as occurring after copulation; however, my film analysis revealed that in both wild and captive copulations, food exchange occurred at or near the time of cloacal contact, and always before the male dismounted.

Courtship feeding has been reported in other solitary, non-parasitic cuckoos, including the Yellow-billed Cuckoo (Hamilton and Hamilton, 1965); Black-billed Cuckoo, *Coccyzus erythropthalmus* (Spencer, 1943); Lesser Coucal, *Centropus bengalensis* (Lack, 1940); and Squirrel Cuckoo, *Piaya cayana* (Skutch, 1966). In contrast to passerine and galliform courtship feeding, which occurs prior to copulation (Andrew, 1961; Stokes and Williams, 1971), food exchange occurs during copulation in these cuckoo species.

An obvious function of courtship food is to induce receptivity in the female (Stokes and Williams, 1971). However, the fact that 25 percent of successful copulations occurred without food suggests that it is not always an essential prerequisite to female receptivity. During pair-formation this function may be more important than later in the season.

Courtship feeding also functions to maintain the pair-bond, especially in those species where both sexes care for the young. Lack's (1940) survey of courtship feeding in birds revealed its occurrence primarily in species that shared parental duties. Among polygynous galliform species, courtship feeding ends with egg-laying, whereas in monogamous species that share nesting duties, it often continues throughout the breeding cycle (Stokes and Williams, 1971). Maintenance of the pair-bond is essential in the Roadrunner, which shares parental duties and often renests.

Royama (1966) indicated that courtship feeding is necessary as nourishment for egg-laying in tits of the genus *Parus.* Perrins (1970) demonstrated that in some birds the breeding seasons are determined by the period of the season at which the female finds enough food to form eggs. In the Roadrunner, a nutritive function is plausible because of the type and large size of the courtship food (vertebrates) compared with the normal adult insectivorous diet (Bryant, 1916). In support of this view, I observed that most courtship food was consumed by wild females just prior to, and during, egg-laying.

Courtship feeding may also serve as an indication of the favorability of the environment for nesting. As successful nesting of the Roadrunner depends upon a large supply of reptiles in the breeding territory (Ohmart, 1973), courtship feeding may indirectly supply information on the nature and quantity of the appropriate food. Thus the female may not lay eggs until the proper stimulation in the form of courtship food is provided. If so, courtship feeding will synchronize nesting and an abundant food supply early in the breeding season. Following the first nesting, the quantity and quality of the courtship food will determine whether renesting occurs.

Since food exchange occurs in cuckoos during cloacal contact, it also may serve as a balancing aid for the male. The male Roadrunner wing-flapped vigorously during cloacal contact, indicating difficulty in balancing during copulation. During this time both sexes grasped the food, possibly giving the male additional support. This was also noted for the Squirrel Cuckoo by Skutch (1966), who observed that the long tail made balancing more difficult during copulation. The male Roadrunner also balanced himself by wing-flapping during copulations that involved no food, although adequate cloacal contact may not have occurred. On one occasion when no food exchange was involved, a wild male grasped the head of the female during cloacal contact. Brockway (1964) reported a similar grasping of the female's head and correlated it with maintaining balance during copulation in the Budgerigar, *Melopsittacus undulatus.*

Associated with courtship feeding in most passerine species is a female display and call resembling the food begging of the young of that species, suggesting that courtship feeding has evolved from general parental feeding behavior (Lack, 1940). Rand (1941) and Calder (1967) observed infantile behavior in the female Roadrunner associated with courtship feeding and consisting of wing-fluttering and the buzzing call typical of young birds. I never observed this behavior pattern in the captive or wild adult females during the present study. The call of the adult Roadrunner that most closely resembled the nestling begging call was the Whine, although the posture accompanying the Whine did not involve wing-fluttering or other infantile behavior. An infantile female courtship display has not been reported in other cuckoos or in galliform species that exhibit courtship feeding (Stokes and Williams, 1971).

Acoustic Signals

Roadrunner acoustic signals reported prior to this study were the Coo (Holterhoff, 1883), Clack (Sutton, 1922), and Whirr (Calder, 1967). The Clack was assumed to be an alarm signal and the Coo a male courtship call (Sutton, *in* Bent, 1940).

TABLE 6
Acoustic Signals of Roadrunner Courtship

Signal	*Sex performing behavior*	*Recipient of behavior*	*Associated behavior*[1]	*Respondent's typical behavior*[2]	*Breeding cycle occurrence*[3]	*Probable functions*	*Other functions or occurrences*
Coo	Male	Alone, female, distant coos, Coo tape, model-tape	Tail-wag, Food-offer, Stick-offer, copulation	**Clack, Whine, Coo, approach,** Bark, Chase, Stick-offer	Pair-formation, nest-building, fledgling care	Attract distant female; stimulate female; sex recognition	Territoriality
Short Coo	Male	Female, model-tape	Tail-wag	**Approach, Clack**	Pair-formation	Same as for Coo	Territoriality
Whirr	Male	Female	Tail-wag[4] copulation	**Vertical Flick, Side Flick, approach**	Pair-formation, nest-building	Stimulate female; sex recognition	Feeding young
Pop	Male	Female	Prance[4]	**Approach**	Pair-formation	Attract female	Startle predators; territoriality
Bark	Female	Alone, distant Barks, male, Coo tape, model-tape		**Bark, Clack, approach,** Coo, Chase	Pair-formation, nest-building, fledgling care	Maintain contact with male; attract male; sex recognition	Territoriality; defense of young

Clack	Male and female	Alone, mate	Pair foraging together, copulation	**Clack,** Bark	All stages	Maintain contact between sexes; indicate sexual receptivity of female	Alarm call; startle reaction
Growl	Male and female	Mate	Pair foraging together, copulation	**Growl,** Whine	Nest-building	Same as for clack	Feeding young; while fledglings leave nest
Whine	Male and female	Mate	Stick-offer, nest-building, nest-site selection	**Stick-offer,** Whine, approach, Growl	Pair-formation, nest-building	Stimulate nest-building; pair-formation	Given by young when attacked by parent
Single-coo	Male and female	Mate	Flick-bow			Reduce aggression when birds are close together	Given by young when approached by parent

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[1] Indicates behaviors given by the performing sex either simultaneously or immediately before or after the signal.

[2] Indicates the typical behavior of the mate following the signal. Behaviors in bold face are the more common ones.

[3] Indicates when in the breeding cycle the signal is most frequent, although most signals occurred throughout the cycle.

[4] Indicates that the behavior always occurs with that signal.

A summary of the acoustic signals of courtship observed in this study is presented in Table 6. Information on the functions of the various signals was derived from various lines of observational evidence and from the tape and model-tape experiments.

The variety and prominence of acoustic signals in Roadrunner courtship, especially during pair-formation, are not surprising when one considers their ecology. Acoustic signals are more effective than visual ones as initial attracting and orientation signals in solitary species with low population densities. The cursorial habit also favors the use of acoustic, rather than visual signals for initial attraction. Also, the lack of anatomical cues for sexual recognition favors the use of acoustic and other behavioral differences to facilitate sexual discrimination.

Acoustic signals reported in some other cuckoos include: a cooing sound in the Yellow-billed Cuckoo (Hamilton and Hamilton, 1965), Common Cuckoo, *Cuculus canorus* (Herrick, 1910), and Common Koel, *Eudynamys scolopacea* (Gosper, 1964); and a bill-snapping noise in the Squirrel Cuckoo and the Lesser Ground Cuckoo, *Morococcyx erythropygus* (Skutch, 1966).

Sexual Recognition

The results of the model experiments indicate that in the precopulatory situation the male Roadrunner does not recognize the female on the basis of anatomical cues, for males exhibited courtship displays to both male and female mounted skins. Evidently the behavioral cue signaling female receptivity was absent, for all models elicited precopulatory behaviors but not mounting. Possibly this cue is the Rear Presentation, the Vertical Flick, or both. Folse (1974) described a slight sexual difference in the color of the postorbital apterium. All models used in this study possessed the male coloration. Thus the results of the female model test may have been confounded by this factor.

If the female Roadrunner does not possess any anatomical cues that identify her, the male Roadrunner may court all Roadrunners and use the subsequent behavioral response of the other bird to identify the sex.

That paired males in all breeding phases courted the model indicates that either a paired male does not recognize his mate, or the male is potentially promiscuous.

The observation that the model was courted only when it was accompanied by the tape of the Coo vocalization is difficult to explain. One possibility is that the unpaired female gives the Coo, although neither the wild paired females nor the captive female exhibited it. Another possible explanation is that although the Coo is a male call, it stimulated other males as well as females. Rendering the Coo may act as a reinforcement in further stimulating the male's sexual behavior.

The responses of the paired females to the models revealed little information concerning sexual recognition. The fact that little or no courtship behavior was exhibited to the model suggested that either critical cues identifying the model as a male were absent, or that the paired female recognizes her mate and is monogamous.

Displacement Behavior

The Preen, Bill-wipe, and Head-scratch behaviors exhibited to the models are all normal comfort movements of the Roadrunner. However, each behavior in response to the model differed from its normal form in consisting of fast, jerky movements, and in being accompanied by the exposure of the postorbital apterium. Such comfort movements appear frequently as displacement behaviors in a variety of organisms and have become ritualized as regular components of courtship in some species (Tinbergen, 1952). Ritualization of these displacement behaviors does not appear to have occurred in the Roadrunner. The frequency of displacement behavior exhibited to the model supports the view that the models failed to supply key stimuli for male and female courtship behavior.

Cyclic Patterns

The Roadrunner continued to copulate after the need for fertilization ceased. This behavior undoubtedly facilitated pair-bond maintenance and prepared the pair for renesting. The resurgence of pair-bond courtship behaviors, especially the acoustic signals, during the fledgling stage also correlated with renesting. Although it cannot be assumed that all pairs renested every season, the results suggested that the potential for renesting is present and will be expressed if the environmental conditions are favorable. One wild male repeatedly courted his mate unsuccessfully although no renesting occurred. The female probably determines whether renesting will occur, based on the quantity of courtship food or some other environmental indicator.

Determinants of Behavior

In the Roadrunner, the appearance of all courtship behaviors in the isolated young indicates a very strong genetic basis for these behaviors, although the experiential factors of self-stimulation and self-feedback were not ruled out. The stereotyped time-motion patterns appearing in captive and wild birds also suggest genetic origins. The courtship responses of captive Roadrunners to humans indicate that species recognition is greatly influenced by early experience.

The absence of most acoustic signals during the juvenile life of the captives was the major difference between captive and wild development. This result suggests that the potential for acoustic production is present during juvenile life, but that experience with the calls of their parents or other adults is necessary for the calls to be given by juveniles. This lack of early experience did not affect the form of the adult calls of the captives, however.

Summary

The courtship behavior of the Greater Roadrunner *(Geococcyx californianus)* was investigated from 1966 to 1972 at field sites in Texas, Oklahoma, and New Mexico and in hand-reared captives. Objectives were to (1) quantify courtship descriptions as much as possible, (2) investigate time-motion patterns of behavioral sequences, (3) understand the functions of these behaviors, (4) delineate changes in the courtship pattern during the breeding cycle, and (5) trace the development of courtship behaviors in juveniles. Field observations and 16 mm films of courtship behaviors formed the basis for these analyses.

The Roadrunner's reproductive cycle begins with a lengthy preliminary courtship characterized by complex sequences of acoustic and visual displays by both sexes. The precopulatory behavior usually involved a tail-wagging display and food presentation by the male, with the female taking the food during cloacal contact. Both sexes exhibited a postcopulatory display. Sexual differences were observed in the courtship of both captive and wild pairs.

Presentation of male and female models in field experiments suggested that behavioral, rather than anatomical, cues function in sexual recognition and stimulation of copulatory behavior.

The courtship pattern of Roadrunners changes as the breeding cycle advances. Pair-bond behavior is most prominent early in the cycle, subsides with nesting, and becomes prominent again during the fledgling stage. Copulation, first occurring in late pair-formation, persists throughout the breeding cycle. The male often omitted precopulatory displays during nesting, but exhibited them again during the fledgling stage. The renesting potential of the pair might account for these breeding cycle changes.

Nine acoustic signals were used during the breeding season, three of which were male-specific. All were simple, low frequency sounds of varying intensities. Acoustic communication between distantly spaced birds involved the louder signals, while the softer signals were exchanged between members of the pair in close proximity. Field and laboratory experiments indicated that the Coo, the prominent male call, served to attract and elicit courtship displays in both sexes. Nesting females were exceptions as they did not show any response to the Coo.

Captive hand-reared birds exhibited typical courtship and copulatory displays to humans. That these behaviors appeared in hand-reared birds and also in an incubator-hatched male reared in isolation from other Roadrunners indicated their strong genetic basis.

Certain motor patterns and acoustic signals of preliminary and precopulatory courtship appeared in captive and wild juveniles, although not in a sexual context.

Acknowledgments

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P.D. Whitson assisted with field observations, filming, and the final drawings, and provided constant encouragement during the course of the study. C.C. Carpenter provided stimulation and encouragement as major professor for the dissertation. G.M. Sutton provided access to his literature files and field notes and rendered encouragement. Staff members of Big Bend National Park and the University of Oklahoma Biological Station provided research facilities and living quarters during a portion of the study. The University of Northern Iowa provided secretarial and graphic services.

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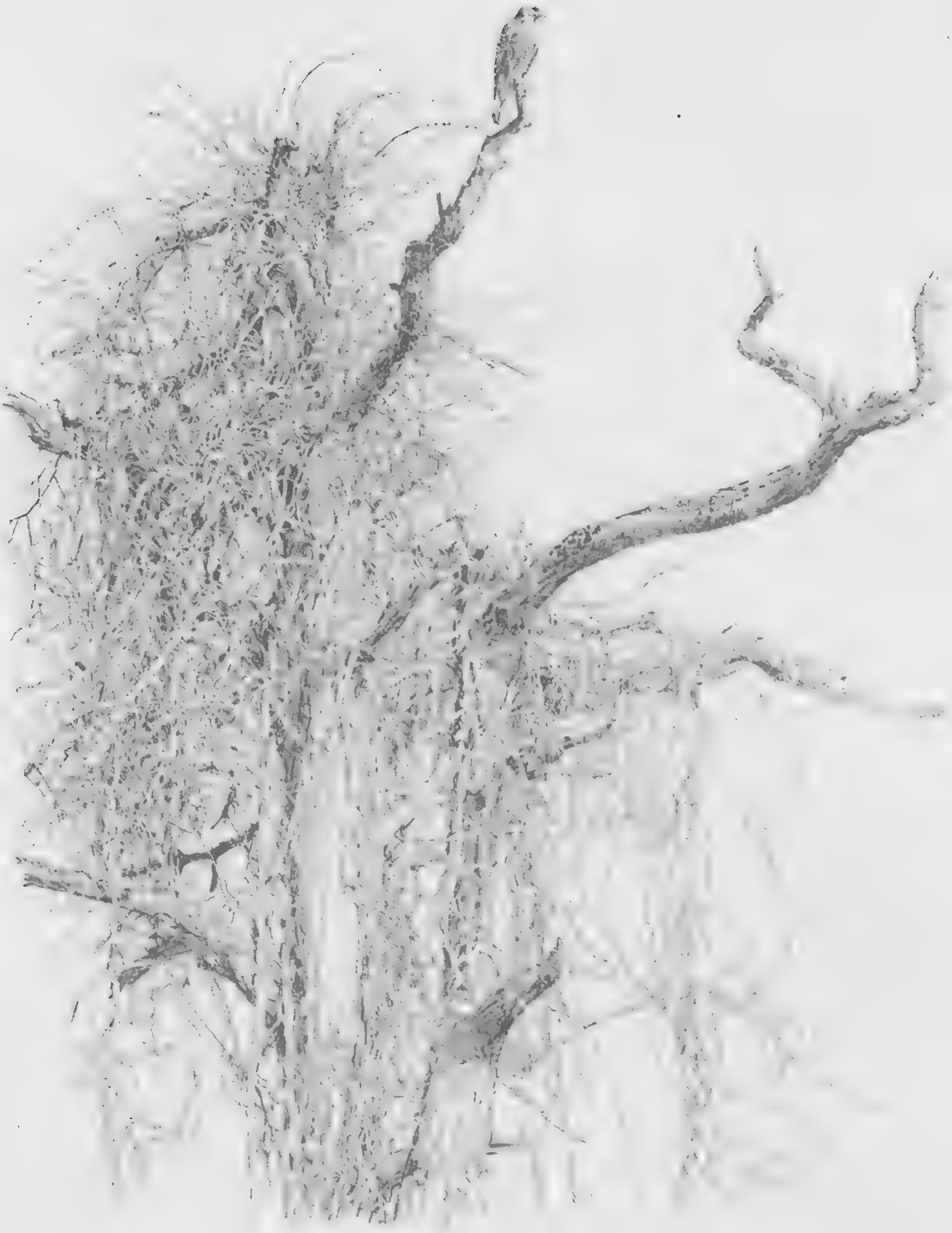

Red-shouldered Hawk, *Buteo lineatus*. Drawing by Ted Lewin.

HAND-REARING HAWKS AND OWLS—SOME COMPARISONS

Frederick and Frances Hamerstrom

Photographs by the senior author

Rearing raptors for reintroduction has become a common and effective method for saving endangered species, thanks largely to techniques developed at Cornell's Laboratory of Ornithology under the direction of Dr. Tom Cade, James Weaver, and their associates.

In recent years, we have reared and reintroduced a number of raptors in Wisconsin, including Marsh Hawks or Harriers (*Circus cyaneus*), Red-tailed Hawks (*Buteo jamaicensis*), Great Horned Owls (*Bubo virginianus*), and Barred Owls (*Strix varia*). In the photographs that follow, we briefly describe some of our methods and compare the rearing of young owls and hawks.

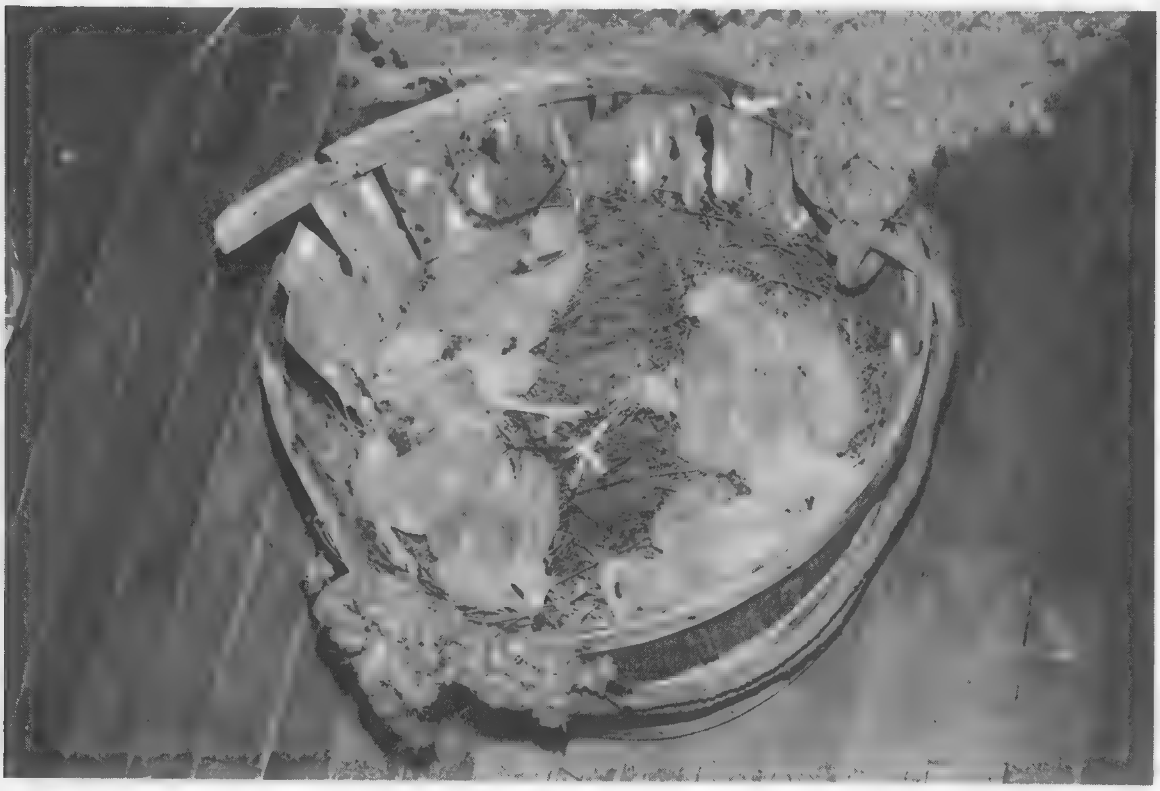

Figure 1. We have hand-reared owls and hawks from one day of age on. We treated all young birds in the same way. By day, we carried them inside our shirts, next to the skin, for the first week or so. At night, they repose in a small basket near the stove, snuggled in old wool socks. When older, and capable of better maintaining their body temperature, they spend their days in a large container out of doors. At night or in inclement weather, the container with its contents is taken indoors.

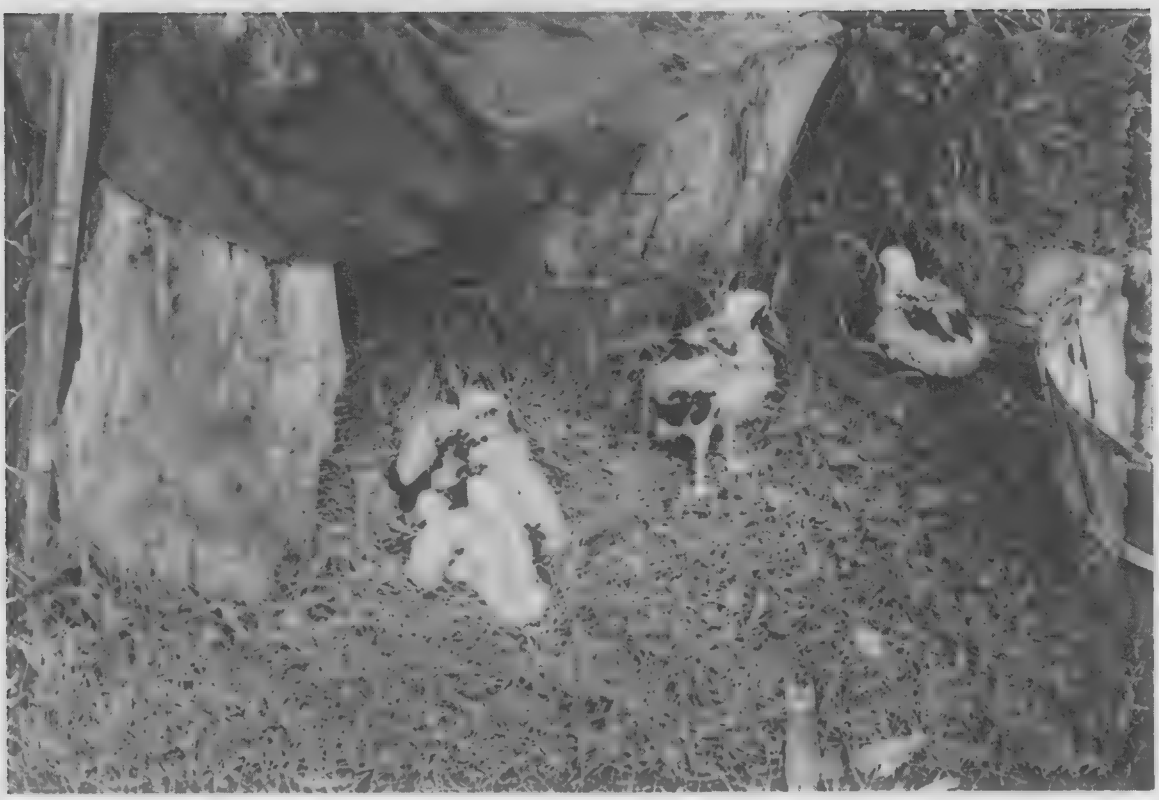

Figure 2. As the young owls and hawks developed, they began to leave the protection of the outdoor container. At this time, we placed a pile of hay near the container for hawks. The hay, vaguely resembling a nest-lining, gives them a sense of place. Owlets do not become attached to a pile of hay; they seek a shady nook instead. We fed the young raptors near their "nest" to strengthen their sense of place.

Figure 3. We made certain to place the "nests" in situations where the immatures could obtain both sunlight and shade. We let them spend as much time as they wished in the sun to guard against ricketts. Young hawks often sunbathed for hours. Even young owls sought the sun's warmth for short periods. The young, especially owls but sometimes Harriers, often sat with their bodies in the shade and their tails turned up and exposed to the sunlight. A young owl that had been deprived of sunlight for several days often sunbathed with its body flattened and wings spread for up to one minute.

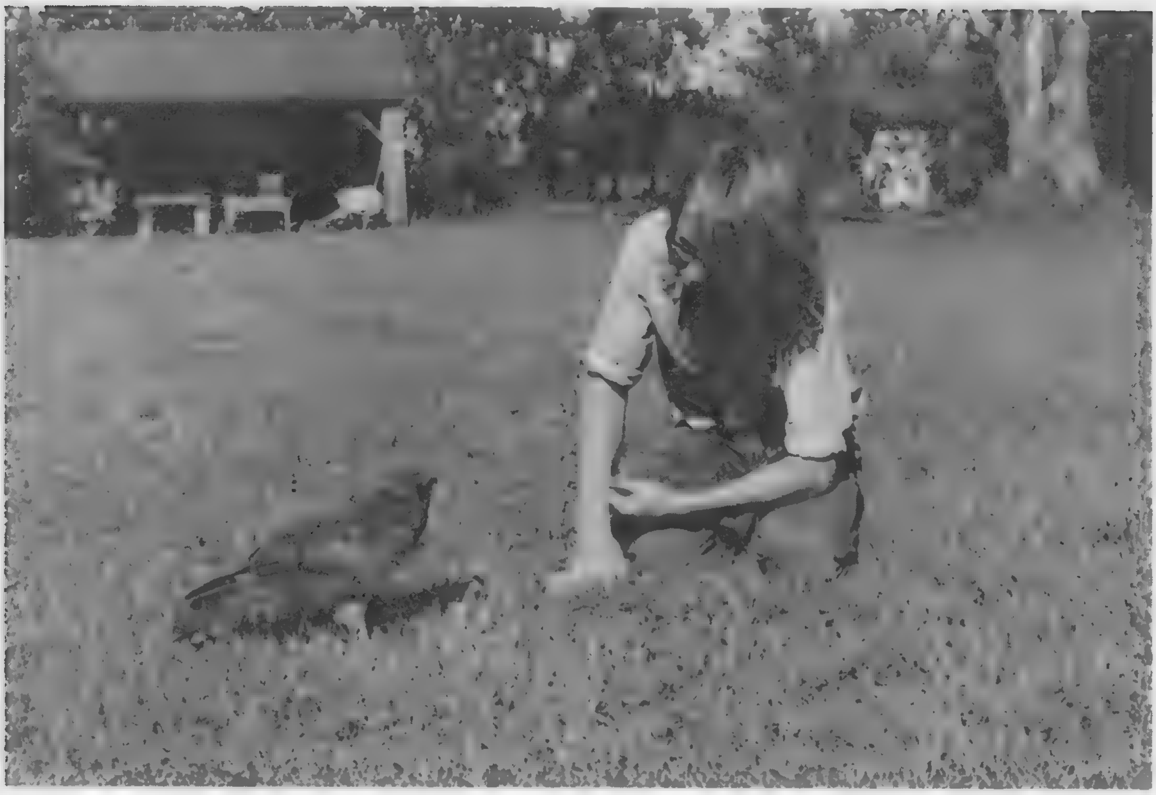

Figure 4. A person hand-rearing a bird of prey often becomes the only foster parent available. There is a danger that these birds may become too tame, although given the proper circumstances, they usually take to the wild readily. Young hawks become particularly tame at the time of fledging, and it is prudent to disassociate them from people and, if possible, to leave them with a conspecific. It is not uncommon for diurnal raptors at this age to accept humans as their preferred mates.

Figures 5, 6, and 7. Great Horned and Barred Owls that we reared became imprinted to humans within the first nine days after hatching. When their flight feathers were undeveloped, they ran down the path to greet our homecoming. Later, they flew to greet us. The young owls often sat on the windowsill waiting for a handout or to be let in.

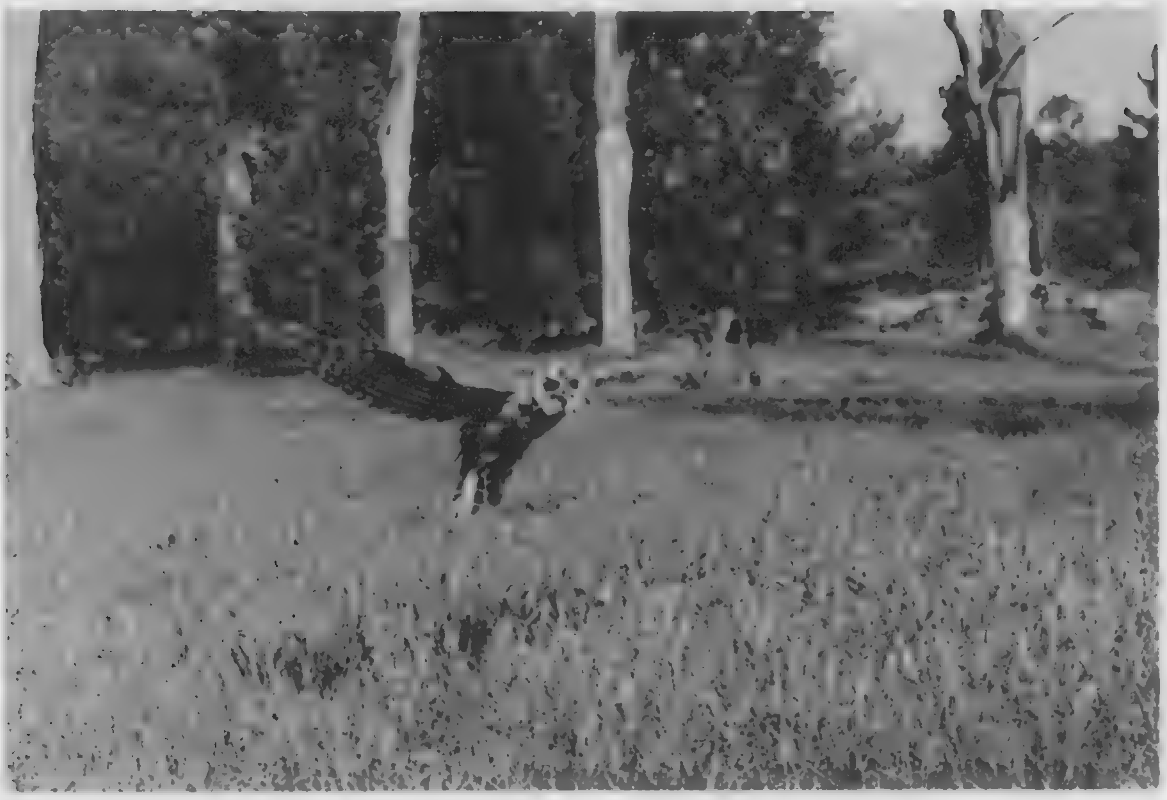

Figure 6.

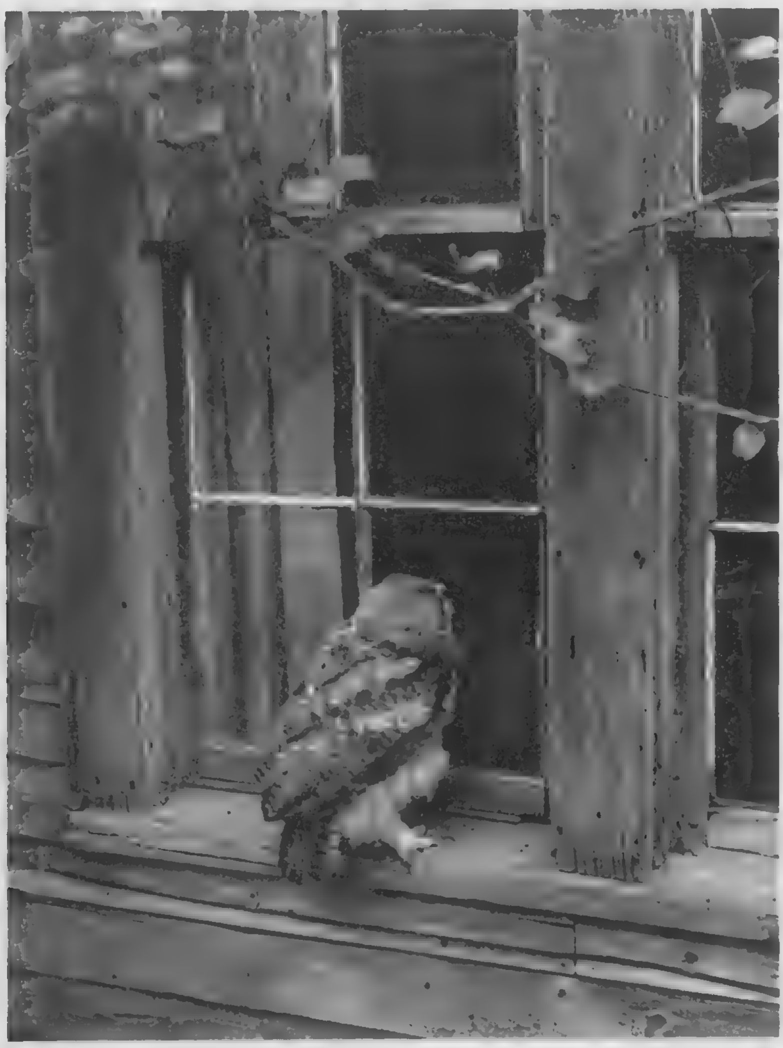

Figure 7.

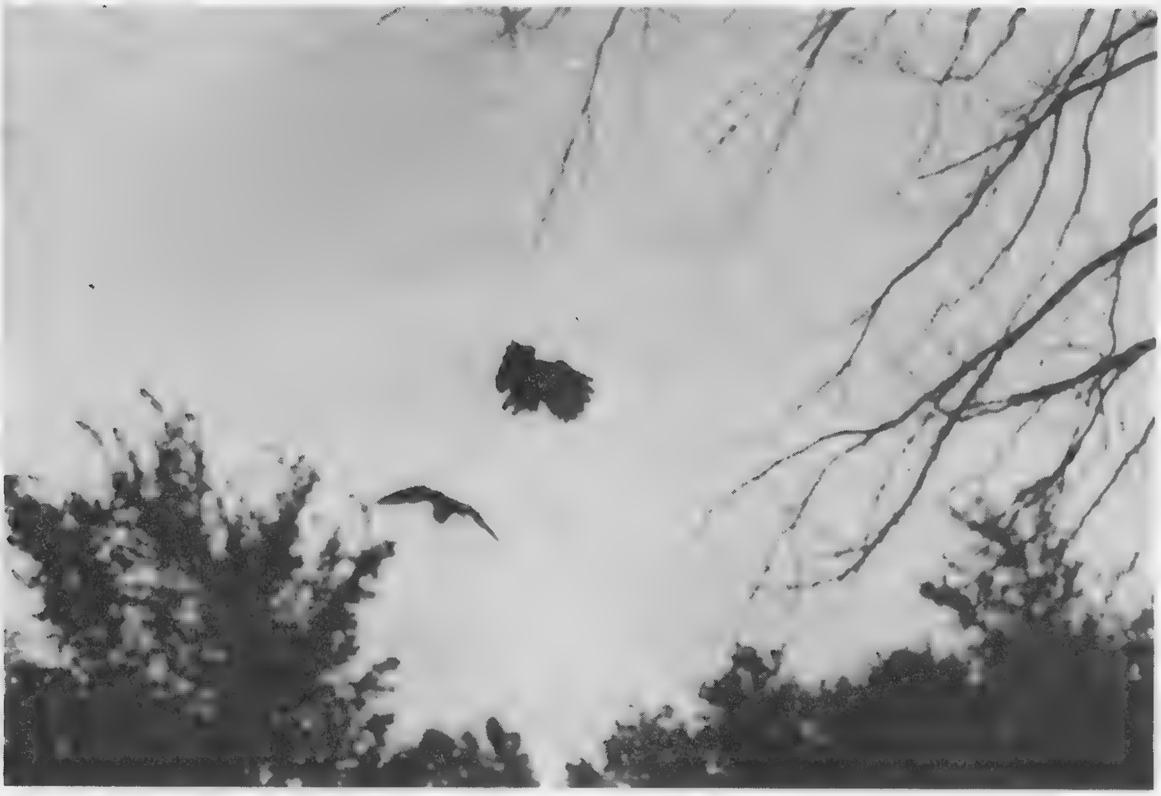

Figure 8. Although young birds of prey often become strongly attached to the human foster parent that rears them, they usually revert readily to the wild state. When we reintroduced both Harriers and a Barred Owl to the wild, called hacking back by the falconer, we watched them "crab" in the air at dusk, their overlapping activity period. First we feared for the owl, then for the hawk. At last we watched the evening show with delight, for neither got hurt.

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Secretary Bird, *Sagittarius serpentarius.* Drawing by Peter Goll.

COMPLEX SONG REPERTOIRE OF MALE LONG-BILLED MARSH WRENS IN EASTERN WASHINGTON

JARED VERNER

Numerous recent studies of singing behavior in birds have documented a wide range of interspecific variability with respect to (1) the numbers of different song types characteristic of individuals and populations, (2) the manner in which various song types are arranged in song performances, and (3) the presence or absence of correlations between specific song types and behavioral states of the singer (for a recent review see Bertram, 1970:173-176). These variations have not been adequately explained. The nearest to a unifying hypothesis thus far advanced is Hartshorne's (1956, 1958, 1973) "monotony threshold," based on the tenet that songs of a singing bird must register meaningfully in the brains of conspecifics within hearing range. He believes nearby birds might adapt by filtering out oft-repeated and monotonous themes. Hartshorne supports his hypothesis by developing the concepts of continuity and variety in song performances of birds and by observed relationships between these concepts.

Continuous singers are those with few, short pauses between songs or vocal utterances so that in a given song performance a high percentage of time is spent singing. Variety results from use of different song types by a given bird: "immediate variety" when different sounds follow one another in sequence, "eventual variety" when the same sound is repeated several times before another is introduced. Hartshorne convincingly supports his anti-monotony hypothesis by showing a marked positive correlation between continuity and variety in song performances of a large number of bird species from around the world (see especially Hartshorne, 1973:124-130). Other authorities, too, have provided support for the anti-monotony hypothesis (e.g., see Bertram, 1970; Dixon, 1969; Gompertz, 1961; Kroodsma, in press; Thorpe, 1961; and Wildenthal, 1965).

The pattern of song type delivery of relatively few bird species fits Hartshorne's classification of high immediate variety, in the sense that each song type or vocal utterance in a sequence differs from the one preceding. Some examples are Gray Catbird, *Dumetella carolinensis* (Borror, 1964); Mockingbird, *Mimus polyglottos* (Wildenthal, 1965); Brown Thrasher, *Toxostoma rufum* (Borror, 1964); Sage Thrasher, *Oreoscoptes montanus* (J. Fitzgerald, pers. commun.); Mistle Thrush, *Turdus viscivorus* (Isaac and Marler, 1963); North American thrushes in the genus *Catharus* (Borror, 1964; Nelson, 1973); and Long-billed Marsh Wren, *Telmatodytes palustris* (Verner, this study). Repertoires of species such as these permit a different test of the anti-monotony hypothesis. If selection has operated to reduce monotony in a performance of singing behavior, it follows that differences between any two successive songs in an actual sequence should be greater than differences between successive songs in a randomly ordered sequence of song types. Statistical tests are available for determining whether or not this has occurred.

The aims of this paper are (1) to describe the song repertoire of male Long-billed Marsh Wrens based on samples obtained in eastern Washington, (2) to describe sequential arrangement of song types by singing males, (3) to attempt to determine the functional significance of repertoire organization, particularly the extent to which it fits Hartshorne's hypothesis, and (4) to suggest an alternate explanation for evolution of song repertoire variety.

Methods

This report is based on 14 separate recording sessions of seven different male Long-billed Marsh Wrens at Turnbull National Wildlife Refuge, 9.7 kilometers south of Cheney, Spokane County, Washington. Details of recording localities, recording times, dates, sample sizes, and breeding status are summarized in Table 1. Specifics on locations of male subjects are shown in Figure 1. Three pairs of neighboring males were recorded to determine possible effects of neighbors on one another's singing behavior. A distance of approximately 1.6 km separated two sets of neighboring pairs, and both of these were about eight km from a third pair of neighbors. I recorded a seventh subject (one without neighbors) three years later in a territory 4.4 km from the nearest earlier recorded neighboring pair.

Field recordings were made on Uher 1000 Report S and Report L models at a tape speed of 19 millimeters per second, using a Uher 54 microphone mounted on a 10-centimeter parabola. Laboratory analysis employed a Wollensak model T1500 recorder at a tape speed of 19 mm per second and a Kay Electric Company model 6000A Sonagraph at F1-1 and wide band-pass filter settings. I used a Beckman type RS dynograph to obtain uninterrupted paper tapes of field recordings useful in determining time intervals between songs.

Statistical tests were made where appropriate, with alpha level set at 0.05.

Figure 2 presents sonagrams useful in reference to definitions employed in the text as follows:

(1) Song: Any complex sound produced in many different contexts, usually repeated for varying periods of time. The distinction between "song" and "call" in this study conforms to that of other workers (see Armstrong, 1963 and Thorpe, 1961 for more lengthy discussions).

(2) Song type: Any of many distinct types of songs, all examples of each song type being enough alike that all could be assigned to a type without ambiguity.

(3) Performance: Any uninterrupted series of songs by a male, lasting from a few seconds to several minutes.

(4) Note: Any short, uninterrupted sound, as represented by a continuous trace on a sonagram, whether or not frequency changes occurred within the trace.

(5) Introduction: The first portion of song, characterized by no repetition of any note and/or relatively long intervals between notes (usually about 0.05 to 0.25 seconds, occasionally as short as 0.01 second).

(6) Main phrase: Second portion of song, characterized by sequential repetition of identical notes or note complexes (see "syllable" below) with relatively short intervals (0.01 to 0.08 second) between them.

(7) Syllable: A note or combination of notes in the main phrase. In song types with the main phrase composed of one note uttered repeatedly, "note" and "syllable" are identical.

(8) Trill: A sound utterance with syllables repeated about 4.4 to 37 per second, producing a "rattling" sound at the faster rates.

(9) Buzz: A sound utterance with notes (also referred to here as pulses) repeated from about 56 to 267 per second, producing a "buzzing" sound. The distinction between trill and buzz is sharp, as subjects in this study uttered no sounds with note repetition rates from 38 to 55 per second.

(10) Terminal note: Any note terminating a song but which is unlike note(s) of the syllable making up the main phrase.

(11) Terminal buzz: A short buzz (usually 0.05 to 0.15 second) at the end of a song, in rare cases followed by a terminal note.

Song types were classified primarily by repetition rate (trill rate) of the syllable in the main phrase, those with higher rates being given lower song type numbers. This proved to be the fastest system for finding all examples of song types in a sample of several hundred sonagrams, because each type exhibited little variability in trill rate, while different types differed consistently. Other features (those exhibiting little variability) used to identify song types were (1) the structure and order of notes in syllables of the main phrase, (2) the structure of introductory notes, and (3) the presence or absence of terminal buzz, and duration and pulse rate of same if it occurred.

No attempt is made here to describe in quantitative detail all parameters of all song types. My data show that specific details of song structure vary from population to population, from male to male, and from year to year within a population. A detailed description of song types identified in this study would apply only to those particular songs, as they represented repertoires of a few birds at one locality in the past. Instead, I have emphasized those general features of tempo and pitch shared by most or all song types, since they apparently identify the songs as those of Long-billed Marsh Wrens.

Song Characteristics

Songs of the six male Long-billed Marsh Wrens sampled in this study yielded 127 song types (Male 4 excluded for reasons given below). Each song

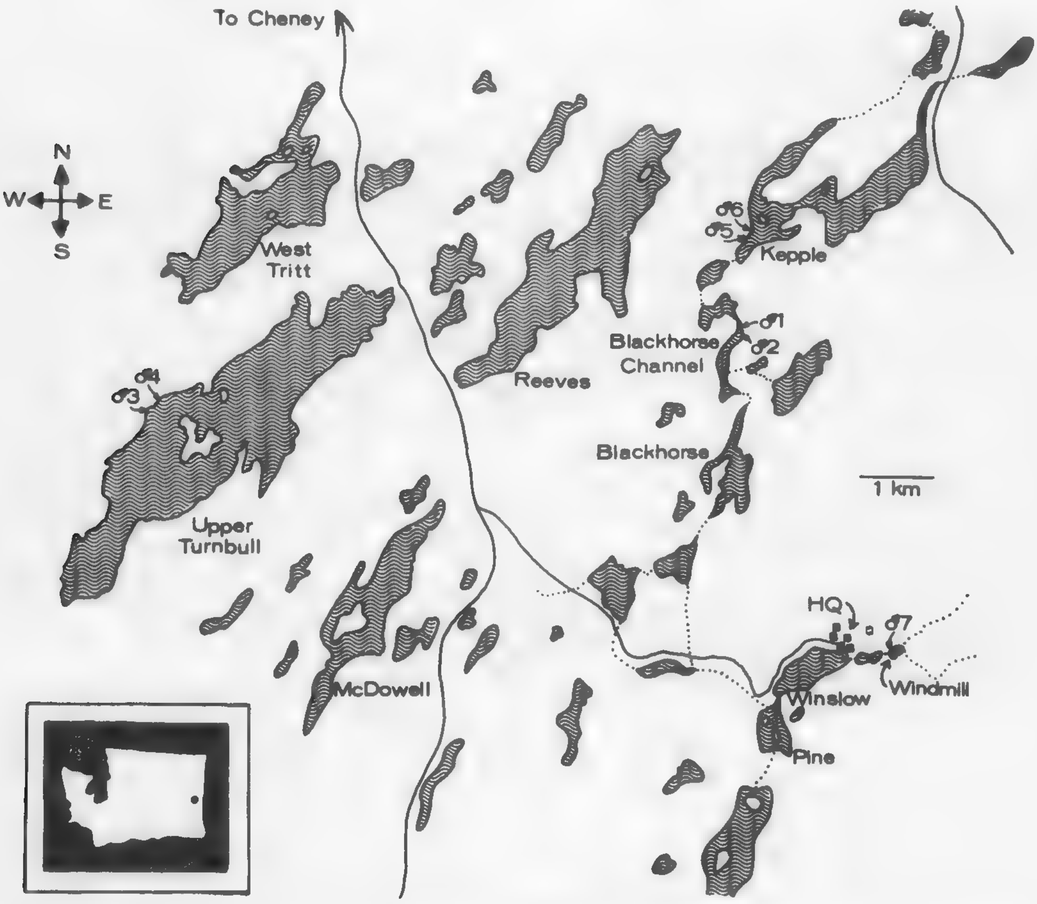

Figure 1. Map of portion of Turnbull National Wildlife Refuge with locations of recorded males indicated by arrows; small inset map of Washington shows general location of the refuge near the east central edge of the state.

TABLE 1
Details of Recording Times, Dates, Sample Sizes, etc.

Male	*Locality*	*Date*	*Time of day*[1]	*Sample designation*	*Number of songs recorded*	*Breeding status*
1	Blackhorse Channel	22 May 1964	04:10-04:45	1A	324	Unmated; 10 courting nest sites
2	Blackhorse Channel	22 May 1964	03:30-04:00	2A	468	Monogamous; five courting nest sites; seven eggs in one nest; laying in progress on first recording date, early incubation on second.
2	Blackhorse Channel	26 May 1964	10:00-10:45	2B	405	
2	Blackhorse Channel	26 May 1964	11:00-12:00	2C	384	
3	Upper Turnbull Lake	18 May 1964	16:10-17:00	3A	409	Bigamous; nine courting nest sites; seven eggs in one nest, six in another; laying in progress at one during all recording sessions, and laying initiated in other the day following last recording session.
3	Upper Turnbull Lake	19 May 1964	05:45-06:40	3B	176	
3	Upper Turnbull Lake	20 May 1964	04:30-05:15	3C	145	
4	Upper Turnbull Lake	19 May 1964	05:00-05:35	4A	417	Monogamous; ten courting nest sites; seven eggs in one nest; laying began the day after both recording sessions.
4	Upper Turnbull Lake	19 May 1964	15:15-16:05	4B	423	
5	Kepple Lake	24 May 1964	03:45-04:07	5A	448	Bigamous; 11 courting nest sites; seven eggs in one nest, six in another; incubation in progress at one nest, laying on the 24th and incubation on the 25th at the other.
5	Kepple Lake	25 May 1964	11:45-14:30	5B	323	
6	Kepple Lake	23 May 1964	04:00-04:50	6A	380	Monogamous; nine courting nest sites; seven eggs in one nest; incubation in progress during both recording sessions.
6	Kepple Lake	23 May 1964	18:30-19:30	6B	66	
7	Windmill Pond	16 June 1967	06:00-06:30	7A	461	Monogamous; 18 courting nest sites; seven eggs in one nest; incubation in progress on day of recording.

[1] Pacific Standard Time.

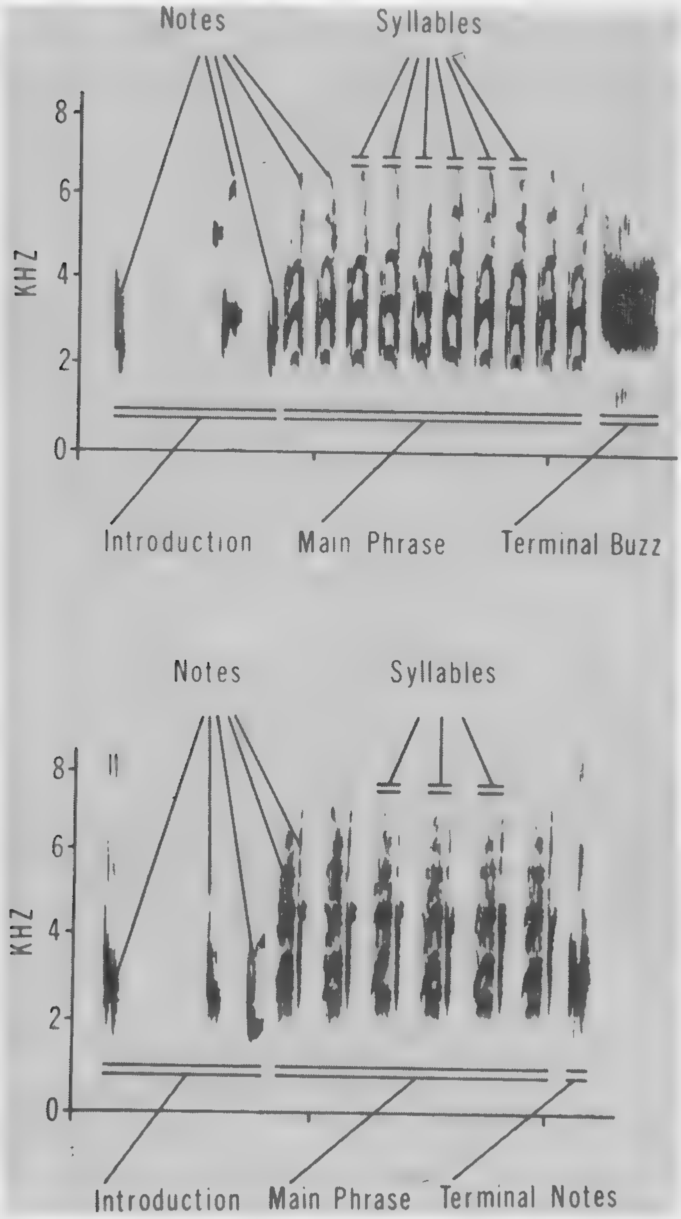

Figure 2. Sample sonagrams of Song Types 43 (above) and 73 (below) with identification of terms used in this study to designate parts of songs.

TABLE 2

Selected Song Parameters, Based on Sample 2A

	Mean	*Range*	*Standard deviation*	*Sample size*
Number of introductory notes	4.4	1-7	1.23	115
Duration of introduction[1]	0.35	0.08-0.68	0.10	468
Number of syllables in phrase	10.12	1-45	7.67	468
Syllables/second	14.78	4.50-121.00	16.16	464
Syllable duration	0.08	<0.01-0.18	0.05	468
Duration of silent interval between syllables	0.03	< 0.01-0.08	0.01	468
Total duration of main phrase	0.72	0.04-1.13	0.19	468
Total song duration	1.14	0.26-1.66	0.25	468

[1] All durations in seconds.

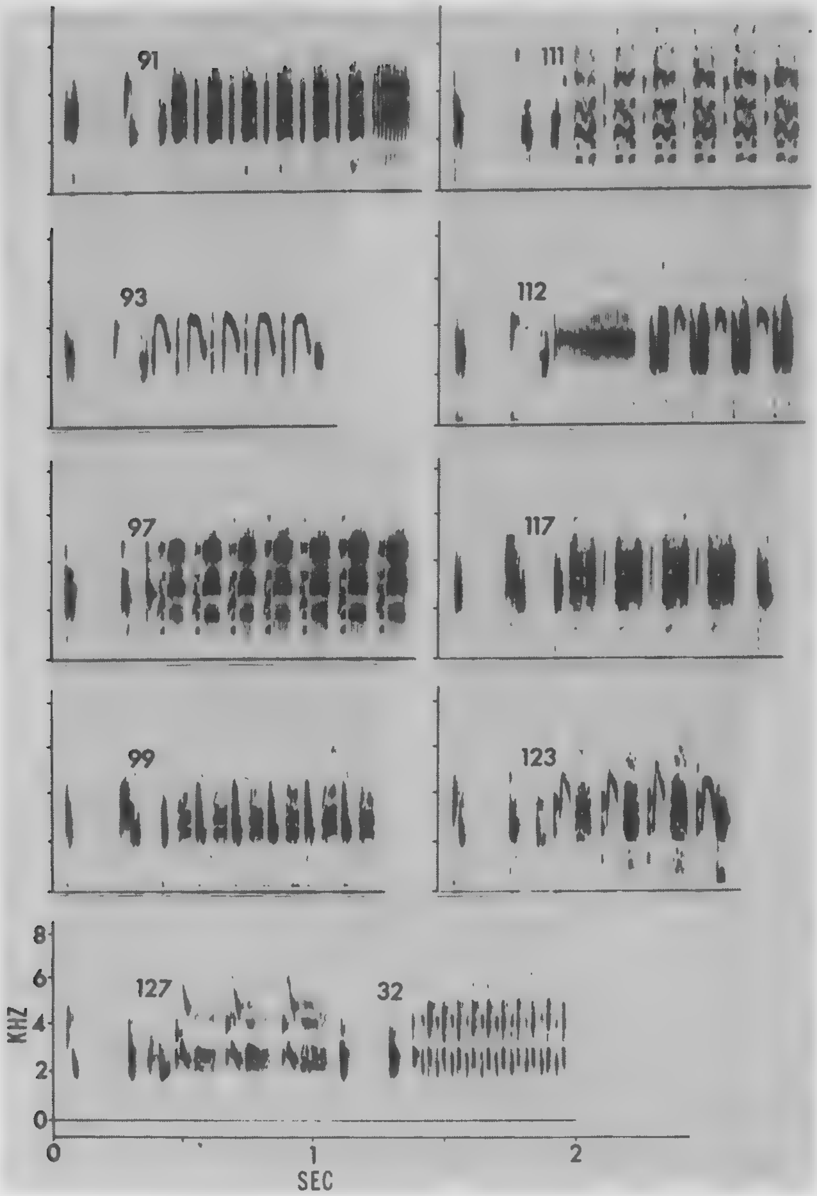

Figure 3. The sonagrams in Figures 3, 4, and 5 show a sample of the repertoire of males described in this paper. Song types are designated by numbers placed on each sonagram, just above the end of the introduction.

began with a series of one to seven ($\bar{x} = 4.4$, see Table 2) introductory notes, followed immediately by the main phrase. The main phrase consisted of a trilled series of syllables, all alike, of from one to three notes (34 song types contained one-note syllables, 59 contained two-note syllables, and 34 had three-note syllables). Depending on song type, syllables were trilled at rates varying from about 4.4 per second (song type 127) to about 36.8 per second (song type 6), the rate of syllable repetition for any given song type varying only slightly. Song types 1, 2, 3, and 4 were exceptional; instead of having trills they had buzzes as their main phrases (56-150 pulses per second depending on song type). Song type 112 was the only type with two main phrases, the first a buzz (pulse rate 59-69 per second) and the second a trill (see Figure 3).

In all, 3,988 songs were analyzed in this study; 1,755 (44 percent) had terminal buzzes with pulse rates varying from about 57 per second to about 267 per second. However, only 62 song types (48 percent of the total) included a terminal buzz at least once. Typically, those song types with terminal buzzes were sung with the buzz, though sometimes the buzz was left off. Twenty-seven types had buzzes 100 percent of the time; 24 had buzzes 90-99 percent of

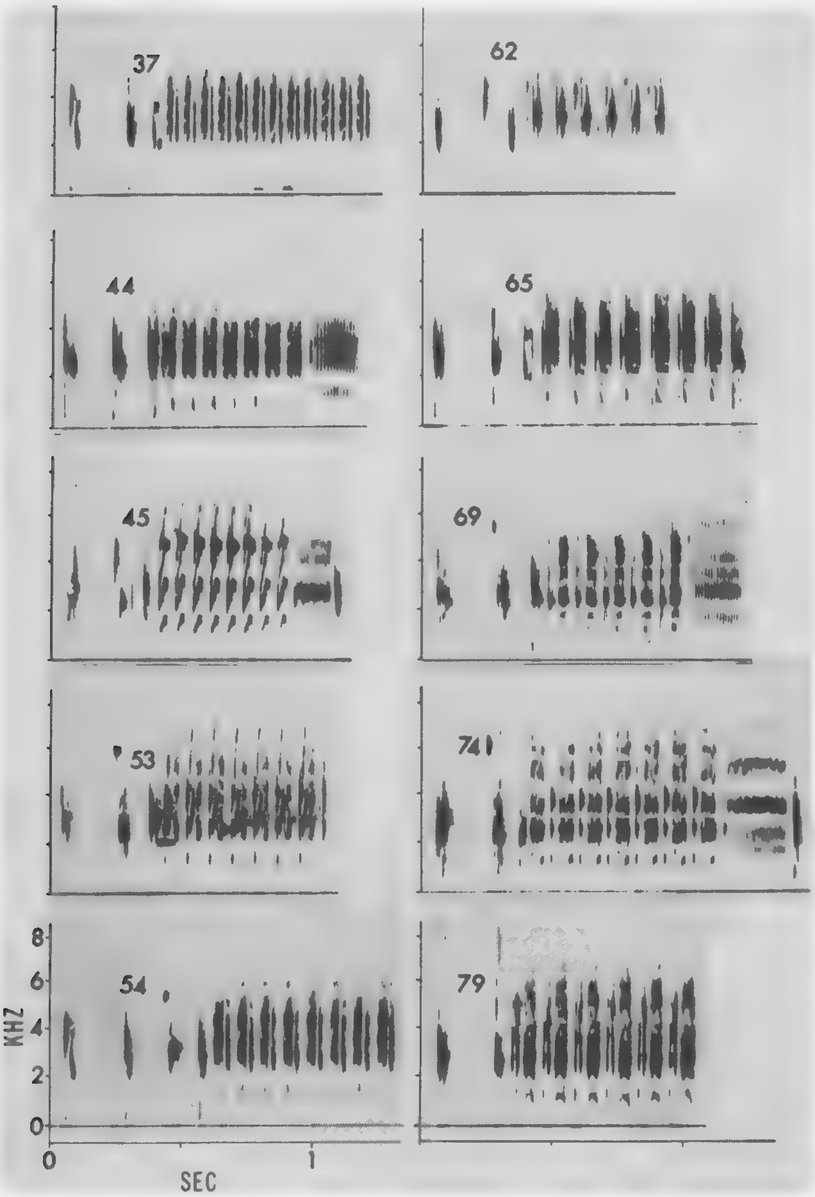

Figure 4. Sonagrams of a sample of the repertoire of males described in this paper. Song types are designated by numbers placed on each sonagram, just above the end of the introduction.

the time; and only five types had buzzes less than 50 percent of the time they were sung; mean frequency of occurrence for all types was 88 percent.

Only 482 of all songs (12 percent) and only 27 song types (21 percent) ended with a terminal note. Unlike the consistency of occurrence noted above for terminal buzzes, only two song types had terminal notes every time they were sung; 15 types (56 percent) with terminal notes had them fewer than half the time they were sung. Mean rate of occurrence was 49 percent for all types exhibiting terminal notes.

Sonagrams of a sample of different song types are shown (Figures 3, 4 and 5) to demonstrate most kinds of variation exhibited in note structure and trill rate, and to show typical frequency ranges of different song types. Based on sample 2A (the largest sample), details of selected song parameters are summarized in Tables 2 and 3. These results show that song duration exhibited a comparatively small ratio of extremes (longest song/shortest song = 6.4), considering the large ratios exhibited by those song features most likely to affect song length; ratios of extremes for introduction duration, phrase duration, and number of syllables per phrase were 8.5, 28.3, and 45.0, respectively. Partial correlations (see Simpson, *et al.*, 1960) show that song duration was due mostly to the length of the introduction and main phrase; when introductions were longer, phrases were shorter, thus tending to equalize overall song length. Variability in phrase duration was reduced because syllable duration and number of syllables in the phrase were negatively correlated.

All songs of all males treated here shared the common features of introduction and main phrase, the two components producing marked auditory contrast. The main phrase of nearly all songs consisted of a trilled series of notes, most sounding like the clicking of one's tongue or the tapping together of two solid objects. Many song types (see Figures 3, 4, and 5) included in their main phrases notes with narrower frequency range, giving them more of a musical quality. In all such songs, however, the musical notes alternated with clicking notes. Rare cases of songs in which the main phrase consisted of only one syllable usually could be associated with some external environmental factor which seemed to inhibit conclusion of the song. Red-winged Blackbirds *(Agelaius phoeniceus)* flying low over the head of a singing male wren commonly had that effect.

Visual inspection of hundreds of sonagrams of Long-billed Marsh Wrens from populations in central Washington (Columbia Basin) and western Wash-

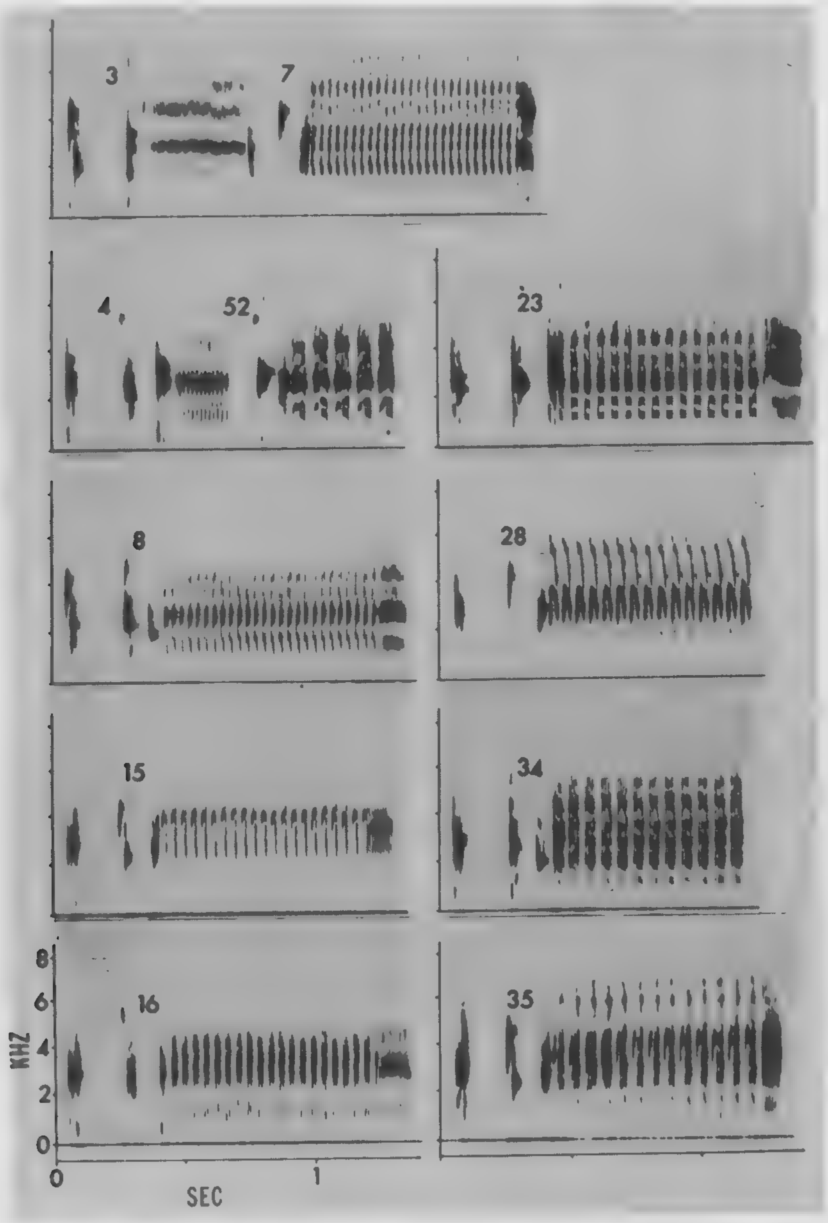

Figure 5. Sonagrams of a sample of the repertoire of males described in this paper. Song types are designated by numbers placed on each sonagram, just above the end of the introduction.

ington (Seattle) showed that their songs, too, always included an introduction and a main phrase. Moreover, the general structural components of notes and their temporal arrangement into songs were like that of the repertoire reported here. Only in the details of note types making up introductions and syllables of main phrases did songs from different populations appear to differ.

Repertoire Size

A cumulative graph (Figure 6) of the number of different song types identified with increasing numbers of songs analyzed provides a means for determining when all different types have been sampled. Figure 6 shows that all males sampled had repertoires of nearly equivalent size and that a sample of about 500 songs from a male was needed to yield about 97 percent of his song types. Males 2, 3, and 5 each used 114 different song types, with respective sample sizes of 1,257, 730, and 771. In order of decreasing sample size, Male 4 sang 104 song types in 840 songs, Male 7 sang 107 types in 461 songs, Male 6 sang 109 types in 446 songs, and Male 1 sang 105 types in 324 songs. Collectively, Males 1, 2, 3, 5, 6, and 7 used a grand total of 127 different song types. This total was only 13 greater than observed for some individual males because most song types were shared by those males. Male 4 was exceptional, since none of his 104 song types could be matched with any of those from any other male sampled.

Figure 7 presents sonagrams of four examples of Song Type 59, all sung by Male 2. Comparison shows that Song Type 59 was repeated with only slight variations, and this was typical of the extent to which each song type was repeated almost identically. Differences among males generally were minor (Figure 8) and involved rare substitutions of note types in the introduction, small differences in note frequency in syllables of the main phrase, and the presence or absence of a terminal buzz. Songs of one type sung at different times by the same male varied in all these same ways, although usually not so much as differences noted between males. Efforts to locate comparable matching of song types from Male 4's repertoire failed. Many of his songs had main phrases similar to those of other males, but introductions did not compare, and the few cases with similar introductions did not compare in main phrases. Generally, magnitude and quality of differences exhibited by Male 4's repertoire were comparable to those exhibited by repertoires of males recorded in other populations in western and central Washington. Hence, Male 4 probably immigrated from another population. Unless otherwise stated, the remainder of this paper analyzes the songs of Males 1, 2, 3, 5, 6, and 7.

All six males shared 83 song types (65 percent of total); five males shared another 23 (18 percent); four males shared five song types (four percent); three males shared six (five percent); two shared three (two percent); and only seven song types (six percent) were unique to any male. Comparison of percentages of shared song types between males, based on any two recorded samples, resulted in a range from 84 percent (sample 7A with sample 5B) to 97 percent (1A with 2A). Neighbors shared a mean of 92 percent of their song types with each other; males 1.6 km apart averaged 90 percent shared song types; and males eight km apart averaged 92 percent shared song types. Thus no evident decline in concurrence of song types between males occurred with increasing distance between their territories.

Even though all males shared most of their song types with other males, they did not sing the various song types with equal frequency. Frequencies by sample of the 20 most often rendered song types were tested for correlation of rank order (by Kendall's tau, Siegel, 1956); samples 3B and 3C were combined because both were equal in all respects except date (see Table 1). Significant correlations taken separately (see Table 4) show no consistent pattern in numbers of positive and negative correlations in comparisons between various morning recordings, between A.M. and P.M. recordings, between neighbors, between birds separated by various distances, or between bigamists and monogamists. Consistent trends are seen in (1) uniformly positive correlations between different samples of the same male and (2) negative correlations between sample 7A and most others. Variations thus were on an individual basis and did not reflect changes in time of day, breeding status, or other parameters. Such differences could contribute to individual distinctiveness.

The significant positive correlations shown for frequency of use of different song types, when comparing different samples from the same male, may obscure another element of the problem. Various males exhibited differences in numbers of times certain song types were sung in different samples. For example, Male 3 sang Song Type 10 five times in samples 3A (P.M., not actively courting, N = 409 songs) and 3B (P.M., actively courting, N = 175) but not once in sample 3C (A.M., actively courting, N = 145). Male 5 sang Type 54 five times in sample 5B (midday, bigamous, incubation at both nests, N = 332) but not once in sample 5A (A.M., bigamous, incubation at one nest, laying at other, N = 448). Song Type 70 occurred five times in sample 5A but not once in 5B, and Type 110 occurred four times in 5A but not once in 5B. Individual variation such as this might be consistently associated with variables internal or external to the male, but neither were my samples large enough for such an analysis nor could all variables possibly influencing males be noted.

Repertoire Organization

Percent Singing Time

Analyses of mean song duration and mean duration of silent intervals between songs (Table 5A, B, and C) indicate that Long-billed Marsh Wrens in this study commonly exceeded the 30 percent level of continuity, making them "semi-continuous" singers by Hartshorne's (1973) classification. Only four

TABLE 3

Partial Correlations of Selected Song Parameters[1]

Parameters	*2*	*3*	*4*	*5*	*6*	*7*
1. Song duration	0.77	0.75	0.17	-0.30	-0.20	-0.16
2. Introduction duration		-0.44	-0.30	0.35	0.14	0.06*[2]
3. Main phrase duration			0.33	-0.24	0.30	0.06*
4. Number of syllables in phrase				0.77	-0.50	-0.03*
5. Syllables per second					0.09*	-0.26
6. Syllable duration						0.09*
7. Duration of intervals between syllables						

[1] Based on Sample 2A. Degrees of freedom (D.F.) = 463 in each case.

[2] Asterisk indicates values lacking statistical significance.

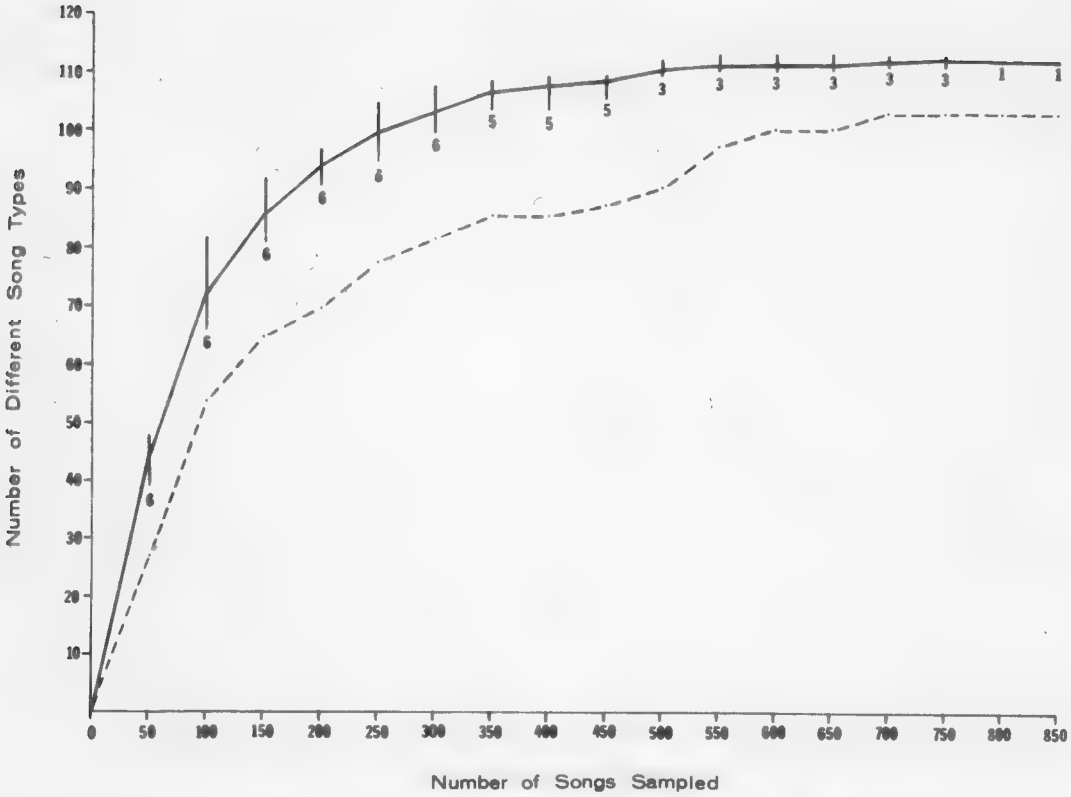

Figure 6. Cumulative graph of the number of different song types used by males in this study. The solid line graphs the mean for Males 1, 2, 3, 5, 6, and 7. Vertical bars at sample points give ranges, and numbers below indicate sample sizes. The dashed line graphs repertoire size of Male 4 (see text for further explanation).

of 12 samples fell below 30 percent continuity. Two of the four exceptions exceeded 29 percent and a third involved a male in active courtship, which inhibits singing. The mean for all sessions was 34 percent (range = 17-44 percent) and a weighted mean based on proportional sample sizes was 32 percent. The percent of time that males sang during sustained performances varied with several factors. Males usually sang more and at higher rates in early morning than during midday, and singing activity increased again toward evening (Verner, 1965, and this study).

Multiple-unit Songs

Two categories of pause duration occurred: single-unit pauses (Table 5B) and multiple-unit pauses (Table 5C). The latter derived from the fact that males commonly sang two or more songs in rapid succession, giving an impression of a longer and/or more complicated song. Table 5B-C shows no overlap in pause durations between units of multiple-unit songs and between songs not linked into multiple units. Figures 3 and 5 present sonagrams of three pairs of song types (3-7, 4-52, and 127-32) linked into typical multiple-unit songs. Typically, songs in multiple units were initiated by introductory notes for any given song type when it was sung alone. I found one exception among 872 samples of songs not first in the multiple unit; in this case introductory notes were omitted altogether from the second song of a multiple unit. Most multiple units consisted of two songs (92 percent of all multiple units) or three songs (7 percent), with four-, five-, and six-song multiple units each comprising less than one percent of the total sample. Most song types (99) occurred in each context, that is, as single units, as first songs in multiple units, and as second or later songs in multiple units. Only three song types never occurred in multiple units and only eight types never occurred as single units.

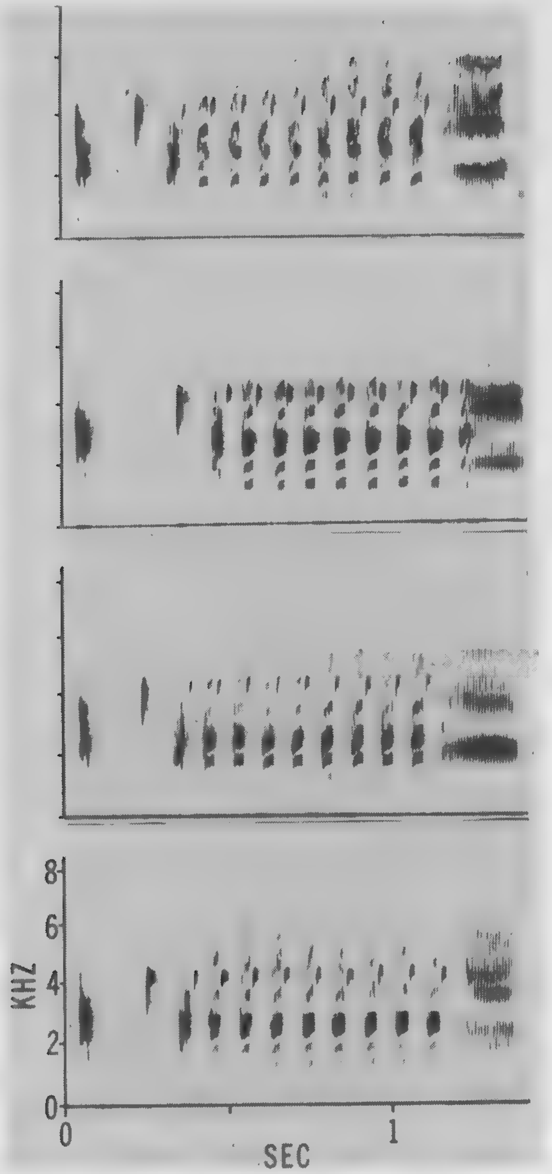

Figure 7. Sonagrams of four different renditions of Song Type 59 by Male 2. Some of the differences apparent in the sonagrams are artefacts resulting from adjustments of the tape recorder and/or sonagraph in the laboratory to obtain as clear a sonagram as possible in each case (cf Greenewalt, 1968: 8-9). Such adjustments were necessary because not all songs were recorded in the field at equal amplitude or with equal clarity.

Many song types exhibited a significant tendency to occur as single units. For example, Type 23 occurred 49 times as a single unit and twice as a third, or later, song of a multiple unit ($P < 0.0001$, by binomial test, Siegel, 1956). Others showed a significant tendency to occur in multiple units, such as Types 12 and 13, which always occurred second or later in multiple units ($P < 0.0001$, $N = 31$ and 27, respectively).

Longer multiple units, five- and six-song complexes, occurred only when a singing male was in close pursuit of a female during active courtship. This does not conflict with an earlier statement that courtship inhibited singing. What little singing occurred during courtship included long multiple units. In such contexts, songs comprising multiple units usually were separated by characteristic notes exhibiting a wide frequency spectrum, notes heard at no other time (Figure 9). Such utterances were unmistakable, giving the impression of a frenzied, breathless effort to congest the maximum possible amount of sound into the shortest possible period of time. I recorded only six sexual pursuits in this study, one of two multiple-unit songs, one of three, three of five, and one of six. In addition to the special form of multiple-unit songs associated with sexual pursuits, males exhibited a strong tendency to sing multiple units when beginning a flight, during flight, and/or immediately after flight. Sixty-nine percent of all songs sung during flight were sung as multiple units, but only 38 percent of songs rendered when not in flight were sung as multiple units. Ten of 11 samples had a higher percentage of songs rendered as multiple units during flights than at other times ($P = 0.0053$, binomial test). No correlation existed between time of day and tendency to sing multiple units (Spearman's $r = 0.11$, $N = 12$).

Some multiple units were composed of songs in which the terminal note of the first song was identical to the first introductory note of the next, but the bird did not sing that note twice in succession when rendering a multiple unit. This fact was established by comparison of such songs in multiple units with songs of the same types when they were sung singly. It seemed reasonable in such cases to assume that no time interval at all separated songs in the multiple unit (see Table 5C).

Song Sequences of Individuals

Males exhibited little tendency to repeat a song type consecutively (hereafter referred to as identical transitions) or even within a short period after it was sung. Table 6 shows that six males sang given song types twice consecutively only 28 times in a sample of 3,988 songs. Only twice did males sing a given song type three times in a row. Male 4 again was exceptional in this respect (Table 6) as he showed a greater tendency to repeat a song type immediately or after only one or two intervening song types. This accounts for the fact that the cumulative curve of different song types did not ascend so rapidly for Male 4 as for other males (Figure 6). Male Long-billed Marsh Wrens in Illinois also exhibit a marked tendency to repeat song types, at least during late afternoon. I have heard as many as six consecutive repetitions by males at Goose Lake Prairie, Grundy County, Illinois.

Mean time elapsed and/or number of songs sung until a given type was repeated were determined for each sample individually. Total duration of a performance was divided by the mean number of times song types were repeated in that sample. Sample 2C was not used in these determinations, because most pause durations between songs were not calculated. Based on the 11 remaining samples, the overall mean time that elapsed before a song type was repeated was 6 minutes 27 seconds (range of means of individual samples: 3

TABLE 4

Kendall's Tau Correlations Between Song Type Frequencies in Different Samples, Using the 20 Most Commonly Sung Song Types.

Sample designation	*2A*	*2B*	*2C*	*3A*	*3BC*	*5A*	*5B*	*6A*	*7A*
1A	.04	.05	.07	-.31[1]	.23	-.01	.02	.05	-.28[1]
2A		.47[3]	.35[2]	-.11	-.35[2]	-.51[3]	-.22	.05	-.14
2B			.39[3]	-.04	-.02	-.27	-.12	.05	-.16
2C				-.03	-.10	-.08	.01	-.08	-.24
3A					.11	.06	.18	.13	.14
3BC						.00	.26[1]	.31[1]	-.02
5A							.07	-.21	.25
5B								.34[2]	-.27[1]
6A									-.20

[1] $0.05 > P > 0.025$
[2] $0.025 > P > 0.01$
[3] $0.01 > P > 0.001$

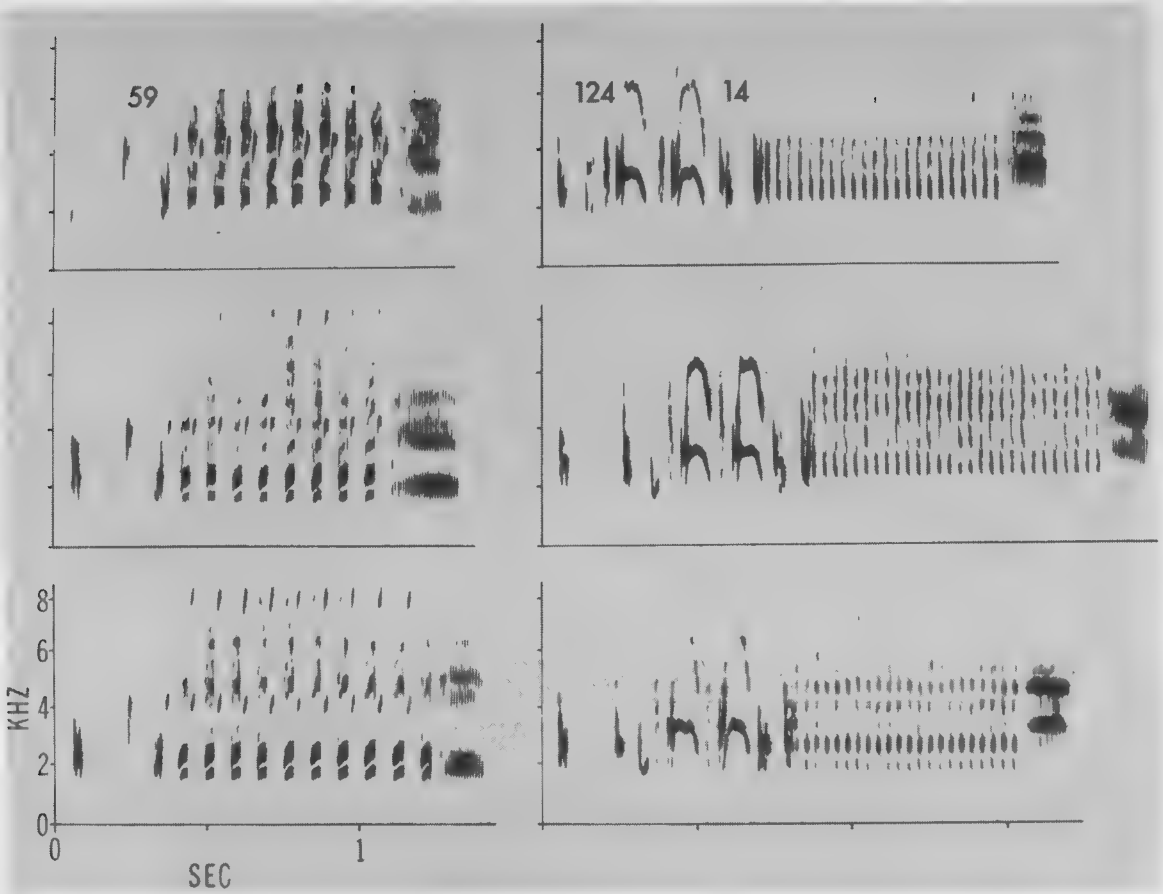

Figure 8. Sonagrams of one rendition each of Song Type 59 by Males 1, 2, and 5 (top to bottom), and one rendition each of Song Types 124 and 14 by Males 2, 3, and 6. Some differences among sonagrams are artefacts, as explained for Figure 7.

minutes 12 seconds to 9 minutes 25 seconds). The shortest repeat time occurred in sample 6B and was probably not representative, as 6B included only 66 songs sung over a period of 4 minutes 14 seconds. The longest repeat time (sample 3B) resulted from inordinately long pauses between songs (see Table 5B) probably associated with prolonged courtship behavior of Male 3. Nine of the 11 samples showed mean time periods required for a song type to be repeated, ranging from 5 minutes 3 seconds to 6 minutes 46 seconds. Males sampled here averaged about 103 to 113 intervening songs before repeating a given type, depending on the size of their repertoire. This fact was complicated because some song types were common and others were rare. Male 1 sang 16 song types only once in a total sample of 324 songs; Male 6 sang nine types once in 446 songs; Male 3 sang six types once in 730 songs; Male 5 sang five types once in 771 songs; and Male 2 sang two types once in 1,257 songs. Repeat intervals for those songs clearly exceeded 113 songs and 6 minutes 27 seconds. Reference to Figure 6 shows that most males repeated some song types even within the first 50 songs sampled, and when 113 songs had been sung, only about 76 different types had been used. An estimate of the number of intervening songs before repetition of the commonest song types was calculated by dividing each sample size by its most frequently repeated song type. Values ranged from 24 (Song Type 17 in sample 3C) to 63 (Song Type 117 in sample 2A) and averaged 39.

The sequence of delivery of various song types, while it conformed to pattern ABCDEFGHI . . . (each letter designating a different song type), was not random in the sense that any song type from an individual's repertoire was equally likely to follow any other type. The total sequence was, instead,

TABLE 5
Duration of Songs and Pauses

Sample	*A. Duration of songs, by samples. Time in seconds.*			*B. Duration of pauses between songs not linked into multiple units, i.e. single units (see text).*			*C. Duration of pauses between units of multiple unit songs. "None" indicates no pause (see text).*		
	$\overline{X} \pm 2SE$	*N*	*Range*	$\overline{X} \pm 2SE$	*N*	*Range*	$\overline{X} \pm 2SE$	*N*	*Range*
1A	1.03 ± 0.02	324	0.46–1.48	3.35 ± 0.24	274	1.24–21.29	0.11 ± 0.04	42	none–0.40
2A	1.14 ± 0.02	468	0.26–1.66	2.37 ± 0.24	306	1.00–30.43	0.13 ± 0.02	158	none–0.32
2B	1.07 ± 0.02	404	0.42–1.67	2.67 ± 0.14	312	0.54–11.54	0.13 ± 0.02	80	none–0.40
2C	1.03 ± 0.02	383	0.42–1.46	2.25 ± 0.24	42	1.14–4.87	0.11 ± 0.02	83	none–0.36
3A	1.23 ± 0.02	409	0.56–1.62	2.30 ± 0.10	345	0.99–7.39	0.09 ± 0.02	51	none–0.40
3B	1.14 ± 0.02	175	0.51–1.65	6.05 ± 0.86	138	1.32–36.05	0.10 ± 0.04	16	none–0.28
3C	1.09 ± 0.04	145	0.36–1.86	3.41 ± 0.56	100	1.22–17.39	0.07 ± 0.02	37	none–0.21
5A	1.24 ± 0.02	448	0.42–1.69	2.00 ± 0.20	335	0.59–26.75	0.10 ± 0.02	105	none–0.35
5B	1.20 ± 0.02	320	0.48–1.78	2.86 ± 0.38	178	1.18–31.56	0.09 ± 0.02	109	none–0.43
6A	1.09 ± 0.02	380	0.56–1.53	2.80 ± 0.24	279	1.02–21.31	0.08 ± 0.02	92	none–0.38
6B	1.13 ± 0.06	66	0.40–1.55	3.63 ± 1.24	44	0.62–28.26	0.07 ± 0.02	17	none–0.19
7A	1.21 ± 0.02	461	0.47–181	2.20 ± 0.06	375	0.80–5.88	0.11 ± 0.02	77	none–0.31

Tabs for heads: 3, 1.32, 13.32, 1.32, 13.32, 1.32, 13.32

Tabs for Chart: 3, 1.32, 5, 3.32, 5, 1.32, 5, 3.32, 5, 1.32, 5, 3.32, 5 markedly stereotyped, with each song type followed by one to several different types. Recordings of Male 2 (bouts 2A, 2B, and 2C combined) contained 1,231 precede-follow song type pairs (i.e., transitions). At one extreme, Male 2 sang Song Type 4 a total of 19 times and in each case followed it with Type 52, giving a transition probability of 1.0 (number of Type 4 to Type 52 transitions divided by number of times Type 4 was sung). Six other song types in samples from Male 2, sung from six to ten times each, also had transition probabilities of 1.0. At the other extreme, Song Type 111 occurred 15 times and was followed by eight different song types with transition probabilities ranging from 0.07 to 0.53. Type 6 occurred 17 times and was followed by eight different song types with transition probabilities ranging from 0.06 to 0.29.

Estimation of the total number of different transitions used by a given male was obtained by graphing cumulative numbers of different transitions against each additional 50 transitions sampled (Figure 10). The curve is asymptotic to the number of different transitions used, and extrapolating plotted curves to points where they should level off yields an estimated mean of 341 different transitions per male, compared with a theoretical maximum of 12,966 (114^2), assuming that any song type was equally likely to be followed by any other and that 114 different types comprised a typical male's repertoire. A similar extrapolation based only on samples 2A, 2B, and 2C, collectively, gave an estimate of 357 different transitions. These extrapolations were made by computer, the curves most closely fitting a second degree parabola. Dividing the mean number of different transitions (341) by the maximum number of different song types for any male (114) indicates that each song type was followed, on the average, by only three of the 113 other song types in the repertoire.

Describing in this manner the consistency with which males sang through their repertoires, repeating many transitions again and again but failing to repeat other transitions, does not portray clearly the true extent of stereotypy evident in the organization of their repertoires. True, a given song type was followed by any of several other different types, producing many low transition probabilities. Superimposed on this variety, however, was a secondary level of consistency easily shown by plotting in detail the precise "pathways" of different song types followed by a singing bird in any given performance. Figure 11 presents such a transition flow diagram for sample 5A. Development of Figure 11 was

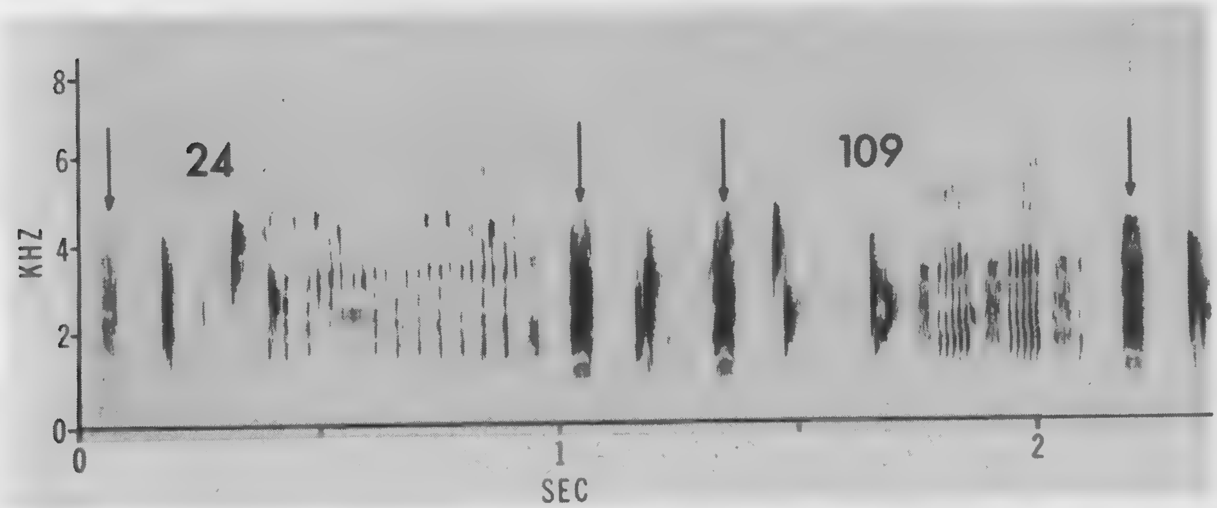

Figure 9. Sonagram of portion of sexual pursuit-singing by Male 3. Song Types 24 and 109 were barely audible on the tape, as Male 3 was in flight and in dense vegetation at the time. Four arrows indicate notes used only during sexual pursuits to link together into a nearly continuous burst of sound long series of songs.

TABLE 6

Number of Times Specific Song Types Were Serially Repeated (Identical Transitions) or Were Repeated with One or a Few Different Song Types Intervening

Sample	*Number of songs in sample*	*Song type sung consecutively*			*Song type repeated with only one intervening type*	*Number of occurrences of a song type in consecutive series of 6 songs*[1]		
		2 times	*3 times*	*4 times*		*2 times*	*3 times*	*4 times*
1A	324	3	0	0	6	14 (4.9)[2]	1	0
2A	468	1	0	0	3	9 (2.0)	0	0
2B	405	2	0	0	3	14 (3.9)	0	0
2C	384	5	0	0	5	15 (5.1)	2	2
3A	409	4	0	0	11	25 (7.0)	0	0
3B	175	4	0	0	8	12 (12.2)	1	0
3C	145	1	0	0	3	7 (6.1)	0	0
4A	417	21	3	1	47	102 (26.6)	28	2
4B	423	13	2	1	51	86 (22.8)	12	5
5A	448	4	1	0	8	15 (3.5)	2	0
5B	323	2	0	0	1	9 (4.1)	0	0
6A	380	1	1	0	10	30 (8.8)	1	0
6B	66	0	0	0	2	2 (4.2)	0	0
7A	461	1	1	0	14	31 (7.3)	2	0

[1] Included in these figures are identical transitions, since, for example, series AABCDE includes type A twice.

[2] Values in parentheses are percentages of all possible consecutive series of six songs in which a given type occurred twice. This is taken as an index of a male's tendency to repeat a theme within a short time period.

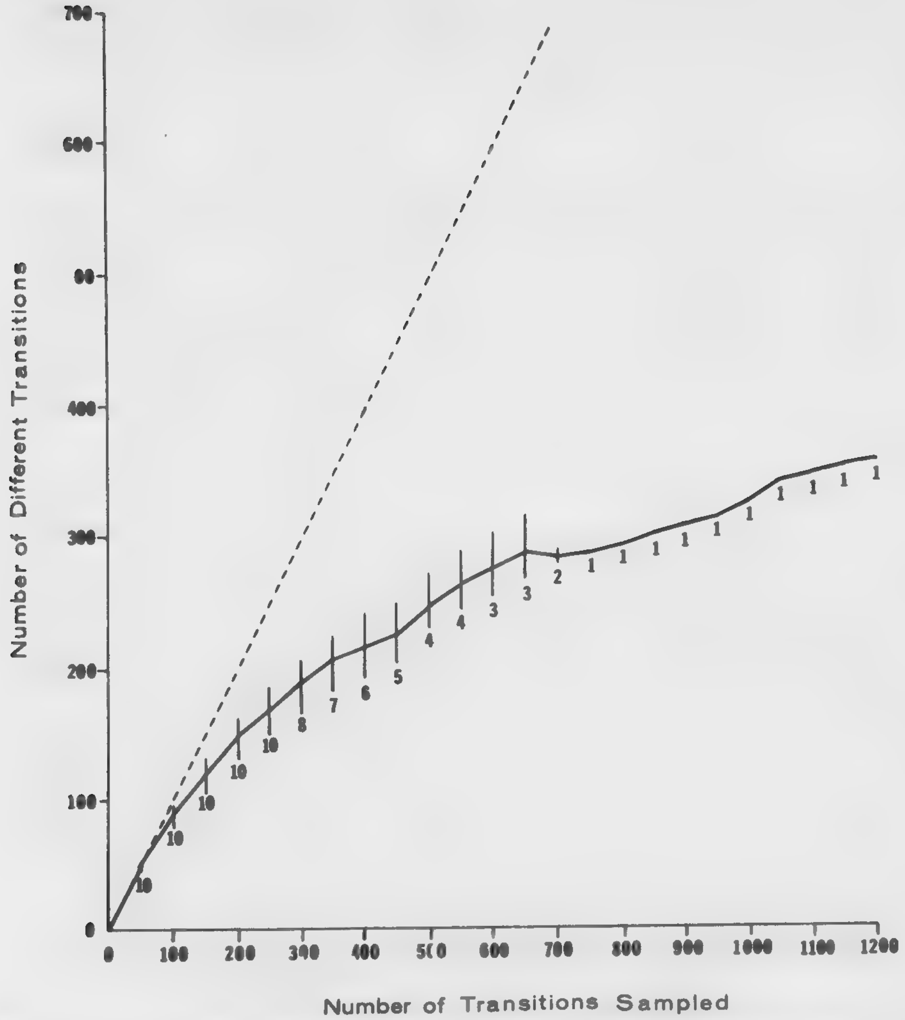

Figure 10. Cumulative graph (solid line) of the number of different transitions used by males reported here. Vertical bars at sample points give ranges, and numbers below indicate sample sizes. The curve drops between 650 and 700 transitions because sample size was reduced and was thus heavily biased by Male 2, whose curve was below average at that point. The dashed line shows expected numbers of transitions if all song types were sung in random order.

based on three overriding principles: (1) keep arrows connecting successive song types as short as possible; (2) maximize clockwise rotation of arrows; and (3) minimize the number of points where arrows intersect.

Figure 11 shows that Male 5's repertoire was organized, with few exceptions, into major "channels" with variable transitions possible throughout those channels. In sample 5A, Male 5 sang through channels forming the perimeter of Figure 11 a total of seven times; he sang through the central channel six times. Transition variations within channels resulted from Male 5's (1) skipping one or more songs in the sequence and going on to another type still in the same general position in the overall sequence, and (2) "back-peddling," that is, repeating a short portion of the usual sequence. Transitions differed also because some song types (e.g., 6, 15, 25, 30, 83, 85, 117, and 125) occurred in two different places in the main channel system. These song types confirm that transition from one song type to another depended on more than just what the first song type was in a transition. At least some transitions were dictated in part by one or more song types occurring prior to the transition in question; that is, this was not a first order Markov chain (see Lemon and Chatfield, 1971) but was more complicated than that. Present data do not allow analysis of this relationship.

My data indicate that transition probabilities generally were not affected by duration of the pauses separating songs in the transitions. Song types that occurred 16 or more times in samples 2A, 2B, and 2C, collectively, were examined for relationships between pause-duration and transition probability. Among single-unit songs with transitions repeated at least five times, I found no correlation between pause-duration ($\bar{x}$ = 2.31 seconds) and transition probability ($\bar{x}$ = 0.41; Spearman's r = 0.18). The mean transition probability was 0.46 (N = 6, range = 0.13-1.0) for song types that occurred only as multiple units. Those types which occurred both as single and multiple units also had a mean transition probability of 0.46 (N = 11, range = 0.13-1.0). Four song types were followed by unusually long pauses on one occasion each, and in only one of the four cases was the transition (Type 99 to Type 17) a marked departure from the usual transitions for Type 99 (Figure 12). Type 114 was followed by Type 47 in every case, even though the pauses between them ranged from 0.12 to 10.76 seconds ($\bar{x}$ = 3.03, N = 11.

An exception to the above pattern occurred in the relationship between pause-duration and the occurrence of identical transitions. Identical transitions were infrequent (Table 6). A multiple unit was involved in only one such case, so it was excluded from this analysis and all pauses discussed here in reference to identical transitions were single-unit pauses. Mean pause-duration between songs in identical transitions (5.71 seconds, N = 29, SD = 4.16) was significantly longer than that (2.60 seconds, N = 50, SD = 1.13) of a sample of five pauses each from the middle of the longest uninterrupted performances from all samples containing identical transitions (t = 3.97; $P < 0.001$). It was also significantly longer than the single pause immediately preceding (3.27, N = 22, SD = 2.09; t = 2.76; $0.01 > P > 0.001$), the five pauses immediately preceding (3.78, N = 96, SD = 4.85; t = 2.11; $0.05 > P > 0.02$), and the five pauses immediately following (3.52, N = 95, SD = 3.97; t = 2.51; $0.02 > P > 0.01$). It was not, however, significantly longer than the single pause immediately following (6.09, N = 22, SD = 4.16; t = 0.13).

Identical transitions occurred significantly more often than randomly within three songs before the end of a performance and three songs after the end of a performance, associated with males interrupting singing to engage in behavior not including singing ($P < 0.0003$ in both cases; binomial test). Finally, five of the 21 different song types involved in identical transitions occurred twice each in such transitions (P = 0.053, 0.048, 0.034, 0.031, and 0.026 in the five cases; binomial test), and one type was used in identical transitions three times (P = 0.0069).

Comparison of Song Sequences Among Individuals

Consistency of song-type sequencing exhibited by individuals extended to all males collectively (except Male 4). Many specific song sequences were shared by two or more males, and some transition probabilities reached or approached 1.0 for all males. For example, Song Type 4 was used by all males, ranging from three to 21 times each, and always was followed by Type 52 (N = 42); Type 124 also was sung by all males (N = 46), being followed by Type 14 on 45 occasions and Type 83 once. At the other extreme, Type 59 was followed by 19 different types, with transition probabilities ranging from 0.02 to 0.31 (N = 62), and only one transition was common to all males.

A better impression of similarities and differences in sequences between males can be gained by carefully comparing Figures 11 and 12. Arrangements of song types in these two figures are identical and were determined specifically for sample 5A. Notice that, in spite of this fact, the sequence in sample 2A fits markedly well into the same schematic arrangement of song types (Male 2's territory was about 1.6 km from Male 5's, so they could not hear one another sing). Extent of sequence dissimilarity between these males is reflected in Figure 12 by the greater number of longer arrows, more points where arrows intersect, and more arrows oriented counter-clockwise. Similar plots were made of other samples, giving similar results — all males sampled shared large numbers of transitions even though separated by as much as eight km and even though Male 7 was recorded three years later.

Taking Song Type 124 as a starting point (see Figures 11 and 12), the time that elapsed before a male sang through his sequence to that point again averaged 3 minutes 4 seconds (range: 1 minute 47 seconds to 5 minutes 10 seconds; N = 20).

Concurrence in song-type ordering between samples was estimated by calculating the percentage of transitions used by one male that also were used by another or by the same male at a different time. In this manner percentages of concurrence could be examined as a function of distances separating males. I calculated such concurrence scores for all possible combinations of two samples, and derived mean scores for males compared with themselves in different samples, with neighbors, with males 1.6 km away, and with males eight km away. Figure 13 shows the results of these comparisons and suggests that similarity in sequences decreased with distance separating males. Standard statistical tests could not be applied to these means, since each mean involved repeated use of each sample in calculating individual scores contributing to means. For example, sample 2A was compared with samples 2B and 2C, sample 2B was compared with samples 2A and 2C, etc., so that six scores were derived from only three samples. Similarly, in calculating means for neighbors, sample 1A was compared with samples 2A, 2B, and 2C, yielding three scores all influenced by sample 1A. Another approach, however, could be used to determine whether or not the observed decreasing concurrence in transitions with distance between males was statistically significant.

Assuming no real differences in sequencing between males as a function of distance, we could reasonably expect that concurrence scores should increase with distance between males as often as they decrease. That is, half the concurrence scores between males separated by eight km should be higher and half lower in comparison with similar concurrence scores between males separated by only 1.6 km (ignoring rare instances of equal concurrence scores). The binomial test can be applied to calculate exact probability of a given number of increases and decreases in concurrence scores with increasing distance between males. Scores obtained for this test were derived by averaging all sample-by-sample concurrence scores between any two males to arrive at a single score for those males; hence only one comparison of Male 1 with Male 2 has been included in the binomial test, and similarly for all other males. Thirteen scores were thus obtained and 11 showed a decrease in concurrence with distance, two showed an increase ($P = 0.0095$). Similarly, to show that any given male's transitions exhibited greater concurrence from sample to sample than in comparisons with samples of other males, a total of 16 scores could be calculated; all 16 showed greater concurrence within a given male than between males ($P = 0.000015$). Figure 13 also includes an estimate of concurrence between Male 7 and other males reported here, but since Male 7 was recorded three years after the others, his scores were not entered into the above computations. Concurrence scores for Male 7 indicate that time may be an even more important factor contributing to differences in transitions than is distance between males, a conclusion supported by the binomial test ($P<0.000001$).

Lower transition concurrence shown by Male 7 may in part be explained by the facts that some of his song types were unique and that he lacked several song types common to all other males. An especially interesting case involved Song Type 46, unique to Male 7, and Song Type 44, sung by all other males but not by Male 7. Figure 14 allows comparison of these two song types, and it can be seen that Type 46 was essentially Type 44 with a short segment missing from the middle of each note in the main phrase. This similarity suggests the possibility of copy error, a possibility supported by the fact that where other males sang Type 44 in their sequences, Male 7 sang Type 46. The two types thus may have been functional equivalents in the sense of their occurrence in the repertoire sequence.

Theme Matching in Countersinging Bouts

It was not possible in the field to identify by ear any of the 127 different song types used by males in this study. However, it often was possible to determine whether or not a song type was sung twice successively by one male or by neighbors singing during the same time period. Many recordings obtained near Seattle, Washington, contained segments in which neighbors were barely audible in the background, and some of those background songs could be sonagraphed. More than 30 percent were of the same type as sung immediately before or afterward by the subject male. With a repertoire in excess of 100 different song types, such a high frequency of matching is most unlikely to occur by chance.

Similarly, during playback experiments I occasionally was able to listen carefully to songs of subject males in relation to those being played by the tape recorder. The importance in these experiments of recording accurately in my field notes other aspects of the subjects' behavior precluded systematic recording of any tendency of subjects to match song types with those played by the recorder. Nonetheless, on six different occasions involving six different experimental subjects in the field, I counted as many as nine consecutive, correct matchings with the recorded tape ($P = 114^{-9}$). Most surprising was the fact that, rather than singing the song type just played by the recorder, the subject *anticipated* each song type to be played next by the recorder, apparently from the previous song or songs, and sang it *before the recorder played it.* One effect of playback thus was to entrain the subject to his position in his total repertoire sequence and to cause him to become leader in a countersinging bout with the recorder.

Differences Between Successive Song Types

Analysis of any tendency by males in this study to maximize contrast between audible components of successive song types was based on careful measurement of several song parameters. Sample 2A was chosen for most of this analysis, since it was one of the longest and contained fewest interruptions in recording continuity. Since song sequencing tended to be comparable from male to male, it seemed reasonable to suppose that a demonstrated tendency toward maximum contrast between successive song types in one performance of one male would indicate a similar tendency in other performances of the same and other males. Conversely, a demonstrated lack of such a tendency in just one sample would

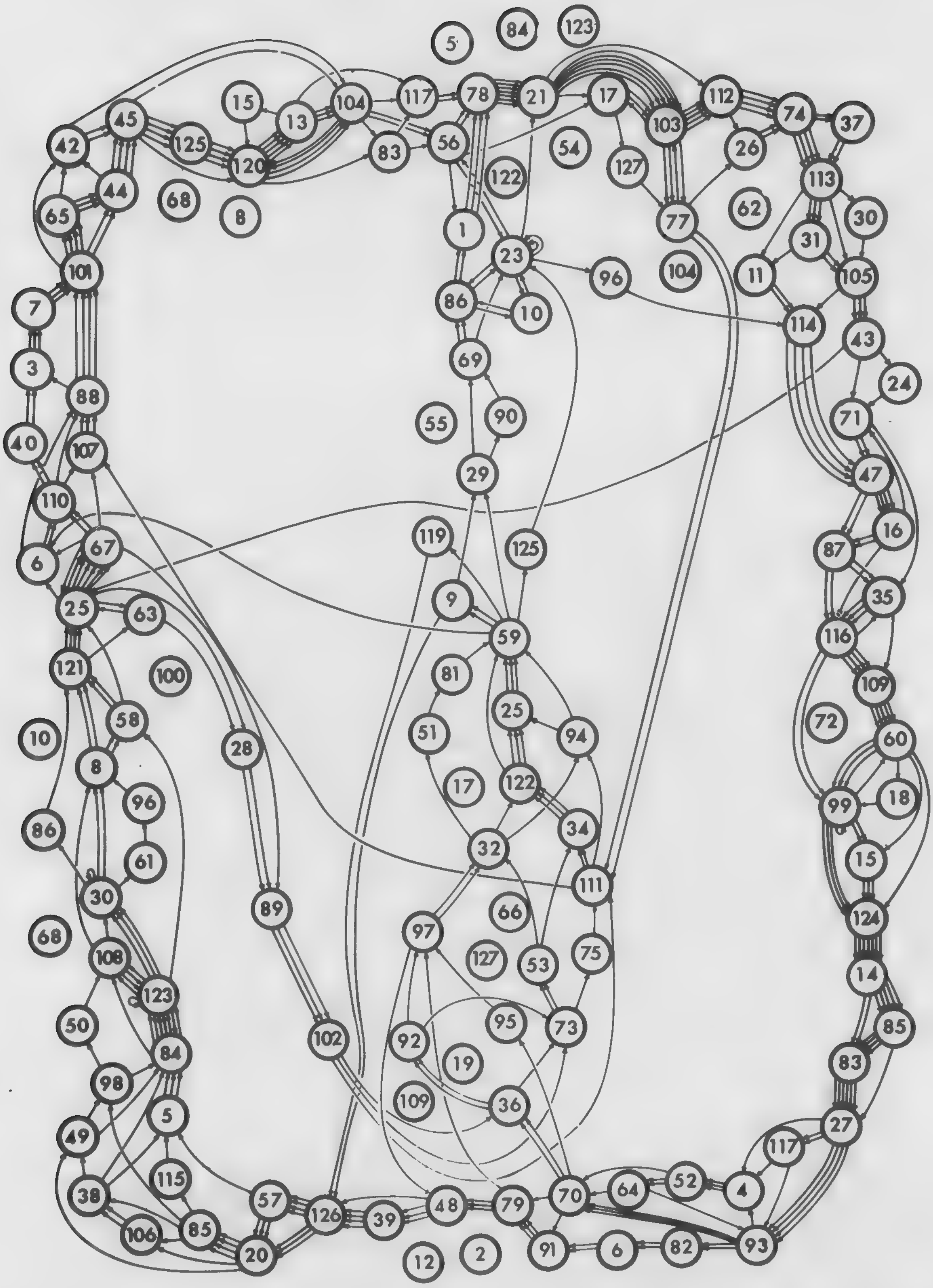

Figure 11. Transition flow diagram of sample 5A. Each circled number designates one song type; each arrow designates one transition. In most instances the number of arrows approaching a given song type equals the number leaving, but exceptions occurred because the recorded sample had a few interruptions, when Male 5 flew out of recording range or stopped singing (see text for further explanation).

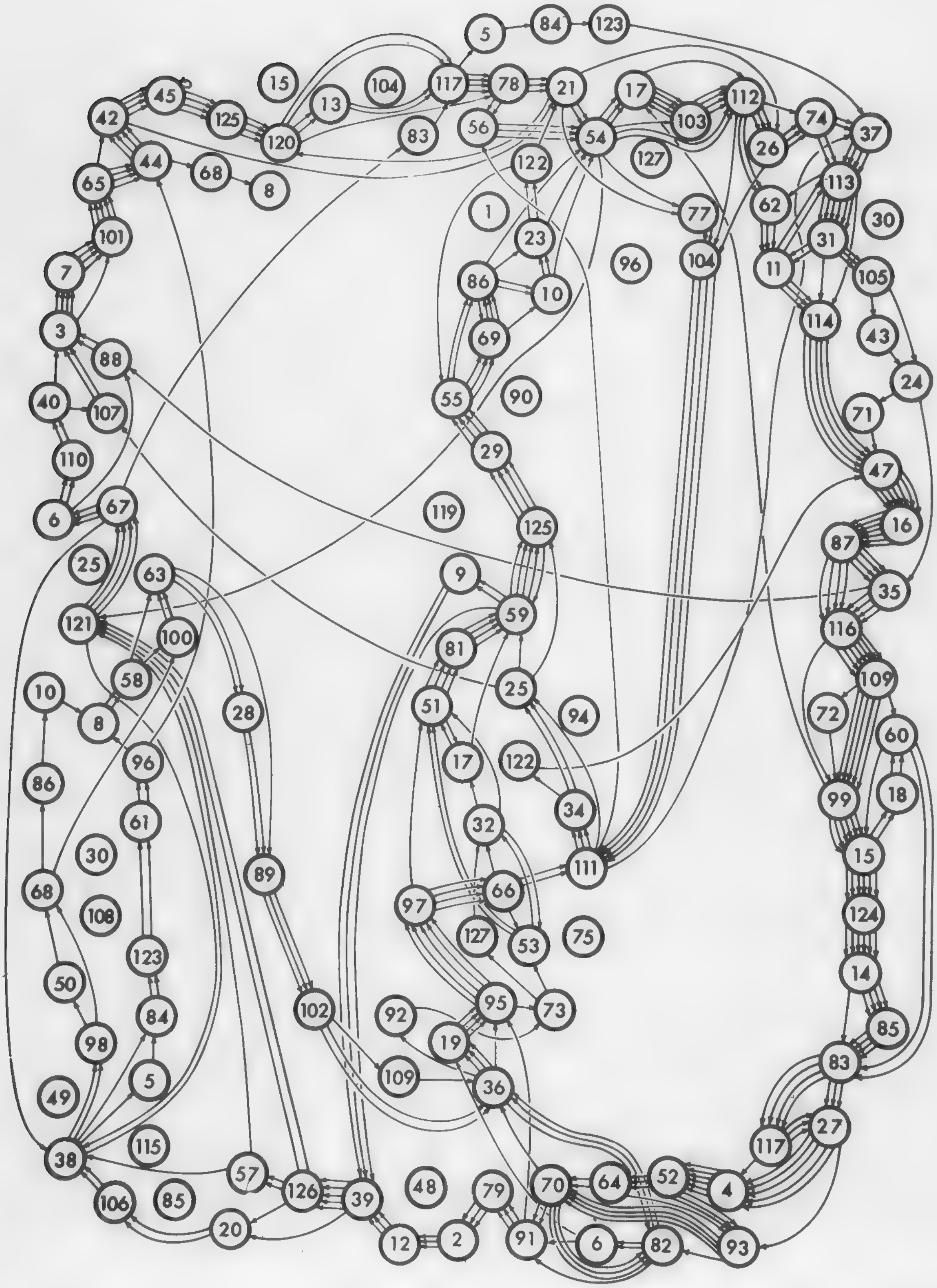

Figure 12. Transition flow diagram of sample 2A. Arrangement of song types on this diagram is identical to that of Figure 11, with which Figure 12 should be carefully compared.

seem sufficient evidence to reject this as a general phenomenon in the population sampled. I selected eleven song parameters for one phase of this analysis, and for each the differences in values between all possible successive pairs of songs were calculated. If songs were so arranged sequentially as to maximize contrast, it follows that difference values obtained from a natural sequence should be significantly greater than difference values generated by a random sequence of the same song types. Each song of sample 2A was assigned a number and a random sequence of all was generated by computer. All values of each parameter of each song were stored in the computer as the random sequence was created, and finally a new set of difference values was derived from the random sequence. Table 7 presents results of these calculations; F tests were applied to all pairs of means. In no case was there a significant tendency for successive songs in the real sequence to differ from one another more than those in the random sequence. Indeed, difference scores for every parameter in real and random sequences, as shown in Table 7, were practically identical.

Other components of song structure permit a simpler approach to analysis of the same question, since they can be handled by the one-sample runs test (Siegel, 1956). Song parameters presenting only two options, such as presence or absence of a terminal buzz, can be evaluated by the runs test for a significant tendency toward clumping together of songs with that parameter (underdispersion), a tendency toward alternation between songs with and without the parameter (overdispersion), or no deviation from random order. Significant overdispersion supports the anti-monotony hypothesis and significant underdispersion is in direct conflict. These results are summarized below:

(1.) Most notes of Long-billed Marsh Wren songs covered a broad frequency spectrum, while some had a narrow frequency range and sounded more musical to the human ear. Each song in sample 2A was classified according to whether it did or did not contain musical notes, and analysis of sequential order of such songs showed them to be significantly overdispersed ($z = 2.13$; $P = 0.016$), supporting the anti-monotony concept.

(2.) Analysis of arrangement of songs with and without terminal buzzes also supported the anti-monotony concept ($z = 3.82$; $P = 0.00007$).

(3.) Songs with and without terminal notes exhibited no significant deviation from random order ($z = -1.19$).

(4.) Multiple-unit songs, contrasted with single-unit songs, exhibited significant underdispersion in sample 2A ($z = -1.87$; $P = 0.031$), contradicting the anti-monotony hypothesis. In sample 1A multiple and single units were significantly overdispersed ($z = 17.8$; $P < 0.00001$), supporting Hartshorne. Seven additional bouts (2B, 2C, 3A, 5A, 5B, 6A, and 7A), all relatively large samples, were similarly analyzed. Bout 3A supported ($z = 19.33$; $P < 0.00003$) and bout 5B contradicted Hartshorne ($z = -4.21$; $P < 0.0003$). None of the five remaining samples departed significantly from random order. Results thus were equivocal, and significant departures from random showed no consistent relationship with time of day and breeding status (Table 1). Hartshorne's hypothesis thus was unequivocally supported by only two of 15 parameters chosen for analysis here.

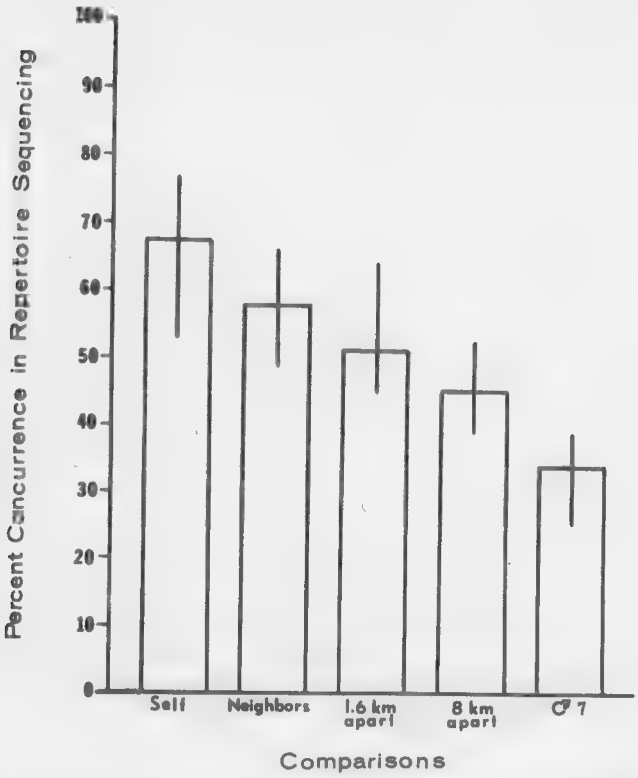

Figure 13. Histograms of percentage concurrence between transitions in song sequence orders of males as a function of distance between them (see text for further explanation).

Contrast of Within-song Components

Contrast in successive utterances in any series of sounds produced by a bird might be achieved by maximizing audible differences within songs as well as between songs. This possibility was explored for marsh wrens by determining correlation coefficients between values for various components of songs where changes in such parameters as dominant frequency and note duration occur. The anti-monotony hypothesis predicts negative correlations, so a 1-tailed test of significance was used. Song features examined were dominant frequencies (Table 7) of first introductory note; first, second, and third notes in syllables of the main phrase; terminal buzzes; and terminal notes. Three of 15 correlations were significant (Table 8); all were negative. In each case the third note in syllables of the main phrase was involved and was thus a point of contrast within songs. This is a puzzling fact in relation to the anti-monotony hypothesis, since only 16 percent of all songs in the sample had three-note syllables in the main phrase. Thus 84 percent of the songs apparently lacked significant internal contrasts at least with respect to dominant frequencies of various notes comprising songs.

Additional internal contrast of songs was provided by the sharp temporal discontinuity created by the comparatively long intervals separating notes of the introduction contrasting with short intervals separating notes of the main phrase, which followed immediately upon completion of the introduction.

Terminal buzzes also added to internal contrast of songs, as most song types with terminal buzzes had higher rates of syllable repetition in the main phrase. Twenty-nine of Song Types 1-32—those with the highest rates of syllable repetition—occurred regularly with terminal buzzes, 18 of Song Types 33-66 had terminal buzzes, as did 11 of Types 67-99, and only four of Types 99-127 ($\chi^2 = 22.0$; $P < 0.005$). Furthermore, song types with the highest rates

TABLE 7

Differences Between Selected Parameters of Successive Songs in an Actual Sequence[1] Compared with a Random Sequence of the Same Song Types

	Real sequence			Random sequence			F score
	$\bar{X}$	*S.D.*	*N*	$\bar{X}$	*S.D.*	*N*	
Song duration (seconds)	0.26	0.203	464	0.29	0.219	463	2.70
Introduction duration	0.11	0.092	464	0.11	0.099	463	0.01
Numbers of syllables in trill	8.08	7.444	464	7.66	7.648	463	0.70
Syllables/second	12.65	18.743	456	12.24	19.660	455	0.00
Syllable duration	0.05	0.038	464	0.05	0.036	463	1.68
Interval duration between syllables	0.01	0.011	464	0.01	0.010	463	0.47
Main phrase duration	0.20	0.163	464	0.21	0.177	463	0.33
D.F.[2] first introductory note	0.53	0.587	464	0.51	0.579	463	0.10
D.F. first syllable note	0.72	0.568	464	0.79	0.587	463	0.70
D.F. final note	0.72	0.583	464	0.75	0.546	463	0.36
D.F. final note minus D.F. first introductory note of next song	0.66	0.622	464	0.67	0.587	463	0.04

[1] Actual sequence from sample 2A.

[2] D.F. = dominant frequency, estimated as mid-point of the darkest trace on sonagram.

of syllable repetition also generally were those with one-note syllables, and those with lowest rates of syllable repetition usually had three-note syllables. One-note syllables provided least variety within syllables; three-note syllables provided most variety. Comparison of the distribution of terminal buzzes among song types with one-note and three-note syllables confirmed a significantly biased distribution in favor of those with one-note syllables ($\chi^2 = 4.94$; $0.05 > P > 0.025$). Thus, internal contrast was effected in songs with one-note syllables by the addition of terminal buzzes, in songs with three-note syllables by differences among notes of each syllable, and possibly in songs with two-note syllables by a combination of these factors (song types with two-note syllables exhibited the predicted frequency of terminal buzzes).

Function of the Complex Repertoire

This study permitted testing certain possibilities that might explain the functional significance of large song repertoires. If one conditionally accepts the view that songs of male birds function to attract potential mates into the territory and repel competing males from the territory, one can argue that one or two song types should serve these functions. Such appears to be the case in a variety of species (see Ficken, 1962; Ficken and Ficken, 1965, 1967; König, 1968; Morse, 1966, 1967, 1970; Nicolai, 1964; Oring, 1968; R.L. Smith, 1959; W.J. Smith, 1969, 1970; and Thielcke and Thielcke, 1970). Evolution of repertoires of more different song types might occur (1) to facilitate recognition of individual males by females and other males; (2) to communicate more specialized sorts of information, with each song type having a different meaning; (3) to permit building of information content into specific song sequences, as word orders in human language; (4) to provide maximum contrast between successive songs, thus minimizing monotony effects proposed by Hartshorne (1956), and/or (5) to maximize attentiveness during counter-singing bouts between neighbors. Each hypothesis is considered below.

Individual Recognition

The ideal repertoire for individual recognition would be a single, unique song type for each male in a population. Some species have repertoires approaching this, though there is some overlapping of song types between males, as in the Chipping Sparrow, *Spizella passerina* (Borror, 1959, 1961, 1967; Marler and Isaac, 1960); Slate-colored Junco, *Junco hyemalis* (Borror, 1967); and Common Yellowthroat, *Geothlypis trichas* (Borror, 1967). Most species do not fit this pattern, and probably for good reason—namely, species recognition is also important. Many species exhibit a single song type common to all males in a given population, usually with slight individual variations. Other species have small song repertoires, typically fewer than ten song types per population, with extensive sharing of types among males. Playback experiments with some of these have shown that males can distinguish songs of neighbors from those of non-neighbors, for example the Ovenbird, *Seiurus aurocapillus* (Weeden and Falls, 1959); Indigo Bunting, *Passerina cyanea* (Emlen, 1971); and White-throated Sparrow, *Zonotrichia albicollis* (Falls, 1969; Lemon and Harris, 1974). These cases suggest that individual distinctiveness in avian song is possible even among males with small repertoires. Indeed, birds apparently can recognize individuals on the basis of distinctiveness in calls (Bertram, 1970; Emlen, 1972; Kok, 1971).

Marler (1960) first suggested that certain parameters of a single song could function in species recognition, while other parameters of the same song could function in individual recognition. This notion has been widely accepted and recently was given experimental support by Emlen (1971). Thus, if individual distinctiveness occurs with small song repertoires, it weakens the argument that large repertoires evolved to provide such distinctiveness. Furthermore, selection only for individual distinctiveness fails to account for other observed features of Long-billed Marsh Wren repertoires: (1) extensive sharing of song types by different males, (2) extensive sharing of transitions by different males, and (3) the tendency of neighbors to match song types when countersinging. This does not deny that a complex repertoire, once evolved for other reasons, could contribute significantly to individual distinctiveness. Individual variations among song types of males reported in this study most likely do contribute to their individual distinctiveness.

Different Song Types with Different Meanings

Smith (1972) identified four song types apparently with different messages in Carolina Chickadees, *Parus carolinensis* (for other references on this species, see Ward and Ward, 1974). Others have presented evidence that several species

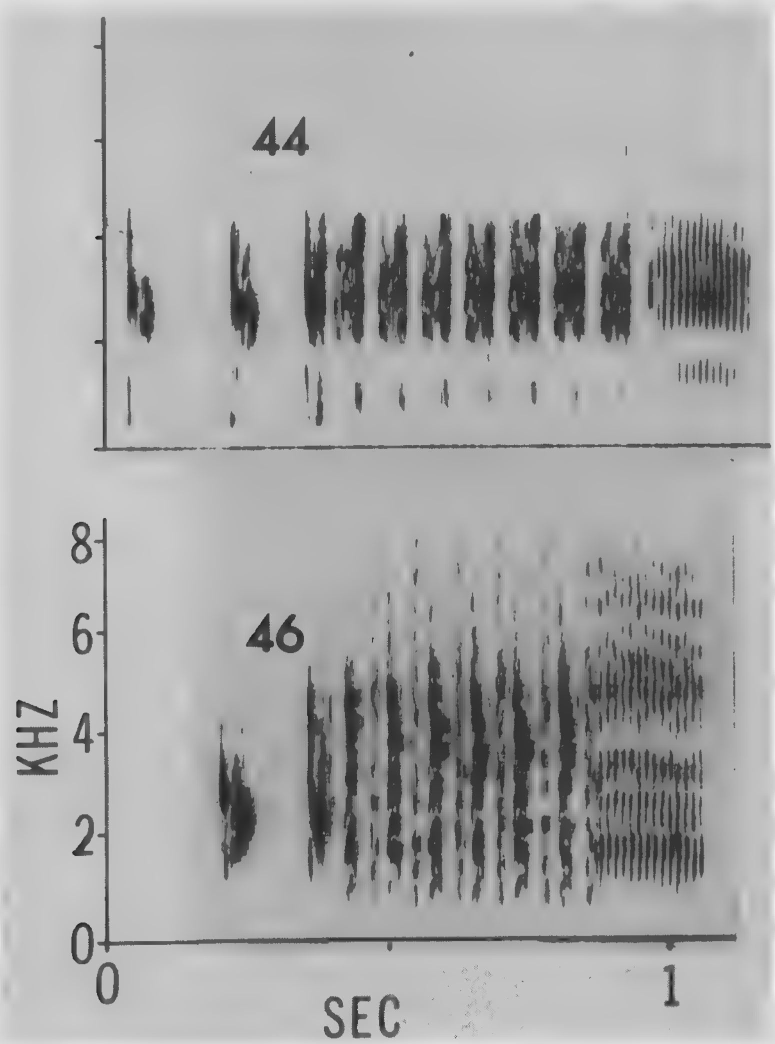

Figure 14. Sonagrams of Song Types 44 and 46 to show that Type 46 (unique to Male 7) may represent a copy error of Type 44. Note that the two types are alike in most respects. The two-note syllables of Type 46 could be derived from the one-note syllables of Type 44 by leaving out the center portion. Absence of the first introductory note of Type 46 is not typical, as other renditions of Type 46 by Male 7 had the extra introductory note. Moreover, some renditions of Type 44 lacked the first introductory note.

employ two song types, one occurring more frequently in the presence of females, the other more frequently in the presence of males. Craig (1943) found that Eastern Wood Pewees (*Contopus virens*) used four different song types with different frequencies in morning and evening performances. Smith (1969, 1970) suggests functionally different roles for two song types in Eastern Phoebes *(Sayornis phoebe)*, one type associated with aggressive tendencies, the other with nonaggressive tendencies. This problem is rather easily investigated in species such as those indicated above, since their song repertoires are small. Among species with larger repertoires, difficulties of showing correlations between frequency in the use of specific song types and variables internal or external to singing males are multiplied manifold. Some results reported in this study open the possibility that different song types of male Long-billed Marsh Wrens were associated with different tendencies of the singing bird.

Three other lines of evidence, however, suggest that different song types did not convey different messages: (1) Statistical comparison of rank-order frequencies of the most common song types (Table 4) between all possible pairs of samples failed to uncover any pattern clearly associated with anything other than individual variability. (2) Neighbors would not be expected to match song types when countersinging if different types conveyed different messages, unless the neighbors happened to be at similar stages in their breeding cycles and other internal and external influences were similar. I recorded matching of song types in this study between males differing from each other in pairing success, stage of breeding cycle, size of territory, and other parameters. (3) The mean repeat interval for a song type was estimated at about 6.5 minutes. If a male's stage in breeding, for example, were communicated by his singing a certain song type more frequently, his listening audience would need to keep track of his song output over what seems an unusually long time period.

These objections do not negate existence of specific song types with specific messages in the song repertoire of Long-billed Marsh Wrens. The single occurrence of such a song in a bout could be sufficient to convey the message. Relevant here is the fact that identical transitions of Long-billed Marsh Wrens in this study exhibited a significant association with the beginning and end of performances, although most performances were not begun or terminated within three songs of identical transitions. The significant tendency of some identical transitions to be used repeatedly leads to speculation that there were certain places in the overall repertoire sequence where males tended to end and resume performances. This possibility carries with it the implication that song performance time is rather fixed to multiples of the time (three minutes four seconds) taken to sing once through the sequence. Proper analysis of this problem and the whole question of specific song types with specific messages will require enormous samples of normal singing behavior from a large number of different males in all phases of breeding, accompanied by simultaneous notation of numerous variables potentially influencing the birds. This would be a courageous undertaking, indeed.

Varying Information with Varying Song Type Sequences

There exists the possibility of different sorts of information being conveyed by different sequential arrangements of song types, as in human language. This probably is ruled out by two results reported here: (1) Neighbors showed a marked tendency to use similar song-type sequences even though

TABLE 8

Simple Correlations Between Dominant Frequencies (D.F.) of Various Notes Within Songs

Parameters	*2*	*3*	*4*	*5*	*6*
1. D.F. first introductory note	–0.01	–0.03	–0.20[1]	–0.04	–0.06
2. D.F. first note of syllable		–0.05	–0.27[3]	0.07	0.17
3. D.F. second note of syllable			–0.26[2]	0.01	0.02
4. D.F. third note of syllable				0.00	–0.70
5. D.F. terminal buzz					0.08
6. D.F. terminal note					

[1] $0.05 > P > 0.025$
[2] $0.025 > P > 0.01$
[3] $0.01 > P > 0.005$

they were in different stages of breeding and undoubtedly exposed to different external stimuli. (2) Playback effected entrainment of subjects to a recorded song type sequence. This occurred with subjects in many different situations. Moreover, subjects were entrained to *lead* in countersinging performances with the tape. If song-type ordering were varied to convey different sorts of information, one should not expect to find such stereotypy of sequences as is confirmed by subjects in playback experiments.

Anti-monotony Effect

Hartshorne's anti-monotony hypothesis as an explanation for the evolution of diversity of song repertoire apparently has been widely accepted. I have been unable to locate any references contradicting the hypothesis, either empirically or theoretically. To date, all published evidence has been based on correlations between continuity and variety (see references in introduction). A central purpose of the present investigation has been to examine a different sort of evidence predicted from the anti-monotony hypothesis. Results of this analysis, coupled with other observations, have led me to conclude that anti-monotony effects at best account for only part of the observations of the variety in organization of song repertoires in different bird species.

Monotonous repetition of the same song type, especially at high rates, could reasonably be expected to result in neuronal adaptation in nearby animals. Peripheral and/or central filtering systems exist for a wide variety of sensory stimuli. Evolution of a complex song repertoire, as an adaptation to preclude such filtering, should involve *sequencing* as well as variety of song types. The ideal anti-monotony repertoire would seem to be one in which a given song type is uttered once and then not repeated again for some time, being followed instead by a different song type (Hartshorne's "immediate variety"). A great majority of complex repertoires studied to date involve birds that consecutively repeat one song type many times before switching to a different one (Hartshorne's "eventual variety"). Some of these species, such as the Dark-eyed Junco, *Junco hyemalis oreganus* (Marler, *et al.,* 1962), sing the same song type for long periods, perhaps long enough for monotony effects to be manifest. Inclusion of such species in the array of evidence in support of the anti-monotony hypothesis must at least be fortified with studies of the time period required for filtering effects to occur.

Support for the hypothesis is better sought through analysis of repertoires providing immediate variety, such as that in Long-billed Marsh Wrens. As pointed out earlier, selection for reduced monotony should favor males with comparatively greater differences between audible components of successive song types. Most results presented here do not support this view. Only two of 15 parameters tested supported the prediction. Not all parameters tested, however, contributed equally to a potential for audible distinctiveness between song types. To my hearing, certain parameters were more conspicuous than others, and my subjective ranking of the four most noticeable differences between song types was as follows: (1) contrast between multiple-unit and single-unit songs, (2) presence or absence of terminal buzz, (3) rate of syllable repetition, and (4) occurrence of "musical" notes in syllables of the main phrase. Items 2 and 4 exhibited differences between successive song types significantly greater than would occur with random sequencing of song types, thus supporting Hartshorne. Data on ordering of multiple-unit and single-unit songs provided no support. It was shown that frequency of multiple units correlated with flights and probably also with courtship encounters and singing neighbors, although data were inadequate for confirmation of these relationships. Multiple-unit singing might have other functions incompatible with adding contrast to any series of songs. Thus, results of this phase of my study offered little support for Hartshorne's anti-monotony hypothesis. Better support was found in the fact that individual song types were so structured as to provide internal contrast, suggesting that selection for contrast in any series of marsh wren songs has influenced intra-song parameters as much as, or more than, inter-song parameters.

Kroodsma (in press), in his study of repertoire organization in Rock Wrens *(Salpinctes obsoletus)*, used an approach like that employed here as a means for determining whether or not actual song-type couplets exhibited greater contrast than randomly selected couplets. Only two parameters were measured, using the ten most commonly associated transitions of one male compared to 22 randomly chosen transitions. Both rate of syllable repetition and frequency range exhibited greater contrast between actual transitions than between randomly selected ones ($P = 0.072$ and 0.012 respectively). Kroodsma interpreted his results as supporting Hartshorne, although more parameters of Rock Wren song need to be analyzed. Furthermore, some may decide that a probability of 0.072 is too high to show with confidence that computed differences in rates of syllable repetition were not a result of chance. Nonetheless, this approach has promise as a means for testing the anti-monotony concept independently from continuity-variety correlations. Other species should be treated similarly.

Hartshorne's hypothesis considered selection only on the singer, whereas the listener is an equally vital part of any effective communication. Selection for complexity in song repertoire may be a less likely alternative, at least in some species, than *selection against neural adaptation in listeners.* Unless one assumes that information potentially conveyed to other birds by a singing male is generally not important to them, one can argue that selection favors listeners with the least tendency to filter repetitive, but informative, messages.

The anti-monotony hypothesis does not explain evolution of stereotyped song sequences and the strong tendency for neighboring male Long-billed Marsh Wrens to match song types during countersinging performances.

Countersinging

Song type matching by countersinging neighbors has been suggested for several species, such as the Great Tit, *Parus major* (Gompertz, 1961); Plain

Titmouse, *Parus inornatus* (Dixon, 1969); Black-crested Titmouse, *Parus atricristatus* (Lemon, 1968a); Long-billed Marsh Wren (Verner, this study); Bewick's Wren, *Thryomanes bewickii* (Kroodsma, 1971, 1974); Carolina Wren, *Thryothorus ludovicianus* (Hartshorne, 1973); Blackbird, *Turdus merula* (Hall-Craggs, 1962); Cardinal, *Cardinalis cardinalis* (Lemon, 1968b, 1974); Pyrrhuloxia, *Pyrrhuloxia sinuata* (Lemon and Herzog, 1969); Chaffinch, *Fringilla coelebs* (Hinde, 1958; Thorpe, 1958); Rufous-sided Towhee, *Pipilo erythrophthalmus* (Kroodsma, 1971); and White-crowned Sparrow, *Zonotrichia leucophrys* (Baptista, 1974). Furthermore, it has been noted by many observers that singing neighbors tend to alternate their songs so that both do not sing simultaneously (e.g., Falls, 1969; Marler, 1956); indeed such alternation has been confirmed between two different species (Ficken *et al.*, 1974). Taken together, these observations suggest that countersinging is probably a far more important aspect of avian song behavior than previously suggested. Significantly in this respect, Lemon (1974) commented that for Cardinals "similarity of song-type to their own is essential for the normal response of Cardinals to songs from members of their own species." It is evident that a singing male not only tends to stimulate neighbors to sing during the same period but also that neighbors are totally aware of temporal spacing and varying types of one another's songs. Natural selection for attentiveness during countersinging bouts would reduce or eliminate monotony effects proposed by Hartshorne, and selection against monotony effects could explain evolution both of highly structured countersinging behavior and complex repertoires. Those species with low song rates (i.e. low continuity) could maintain attentiveness by alternating songs with neighbors. Those with higher song rates could maximize attentiveness by varying song types, alternating songs, and matching song types to a lesser or greater extent, perhaps depending on percent of time in actual song. This model integrates the anti-monotony hypothesis with countersinging behavior. I believe it comes closer to accounting for the variety of patterns of song delivery thus far described for birds than does the anti-monotony hypothesis alone.

Dialects

If countersinging is of importance for the reasons suggested above, it may help to explain why sharing of song types appears more commonly between neighbors than between non-neighbors. Such sharing has been reported by many authors cited here and in nearly all other papers I have read on bird song where the analysis was sufficiently detailed to permit critical comparisons. Countersinging may also provide an explanation for song-type matching which now has been reported for several species. Finally, it is relevant to the issue of dialects—their development, maintenance, and significance (see Grimes, 1974).

Some support the view that dialects are maintained because juveniles, during a critical period, learn their songs in the dialect area in which they are reared and that they remain or return there to breed. Such a system could be adaptive in promoting fixation of alleles for traits particularly suited to environmental conditions peculiar to each dialect area (King, 1972; and Nottebohm, 1969). Thielcke (1969) suggests, alternatively, that dialects are maintained because young birds disperse before the end of the critical period for song learning, so their repertoires are influenced by birds singing in areas selected for breeding. Kroodsma (1974) presents clear evidence that this is the case in Bewick's Wrens. Juvenile males established territories in the fall of their first year and exhibited more similarities in song to those of their new neighbors than to those of their fathers or neighbors of their fathers. Yearling male Long-billed Marsh Wrens disperse to breed long distances from territories in which they were reared (Verner, 1971). Thus, the facts (1) that concurrence between transitions in song-type ordering of male marsh wrens decreases with distance separating males, and (2) that neighbors exhibit a strong tendency to match song types when countersinging lend support to Thielcke's interpretation of dialect maintenance.

The observation that playback subjects lead in countersinging duels with the tape recorder is interpreted to indicate that countersinging behavior reflects the dominance/subordinance relationships between neighbors. It seems reasonable to assume that a territorial male would behave in a dominant role to an intruder in his territory. I believe this relationship further highlights the importance of male/male interactions in song behavior and is thus of central importance in the development and maintenance of dialects.

Evolution of Song Rates

An answer to why some species have higher song rates than others awaits accumulation of essential factual details. Surprisingly little adequate information is available on song rates of different bird species, and particularly diurnal and seasonal variations in song rates, considering the ease with which such data can be obtained. Even Hartshorne's wealth of information on continuity of singing by various species has not been determined with scientific precision. Statements such as the following (Hartshorne, 1973: 129) are typical of his mode of documentation: "In sharp contrast is the Yellow-breasted Chat [*Icteria virens*], the most consistently continuous, or nearly continuous, singer in the family, and the only consistently versatile one. Usually seven different phrases, in no fixed order, are used (Bent, 1953: 593) at a rate of ten phrases in 25 seconds (Saunders, 1951: 213). Phrases are short, giving a continuity of perhaps a little over 40 percent. Considering the extreme simplicity of most of the phrases, versatility seems also medium high." A similar procedure led Hartshorne (1956) to assign a continuity of 66 percent to singing of Long-billed Marsh Wrens. Values determined in this study averaged less than half that (32 percent) and ranged from 17 percent to 44 percent, with 10 of 12 scores below 40 percent.

Factors suggested as possibly contributing to increased continuity and/or variety in song repertoires of bird species are: (1) habitats with dense foliage, where song may be more important in communication than visual displays (Marshall, 1950; Wildenthal, 1965); (2) very aggressive territorial defense, especially in dense populations (Mulligan, 1966); (3) singing from elevated song perches, associated with ground foraging (Hartshorne, 1958; 1973); (4) habitats or coloration reducing vulnerability to predators (Armstrong, 1963; Hartshorne, 1973); (5) presence of relatively few other species of song birds in the vicinity, relaxing selection for highly stereotyped, species specific songs (Kroodsma, in press; Lack and Southern, 1949; Marler, 1960; but see Thielcke, 1969); (6) polygynous mating systems, tending to favor continued high song rates after attraction of a first mate (Kroodsma, in press; Verner, 1963). This topic has been reviewed extensively by Hartshorne (1973) but definitive conclusions remain elusive.

Summary

Six male Long-billed Marsh Wrens from the same population in eastern Washington exhibited a repertoire of 127 different song types. Repertoires

for individuals ranged from 107 to 114 different song types, and most types were shared by all males. Individual variations in renderings of the various song types were slight. All song types exhibited characteristic introductions and main phrases, which were similar from type to type in general features of note frequencies and timing within songs but differed in the details of note structure. Songs recorded in other Washington populations also had introductions and main phrases generally like those of the main study population, suggesting that these features are important in species identification.

A given song type was rarely sung consecutively; depending on male and sample, averages from 103-113 other songs, requiring about 6 minutes 27 seconds, intervened between repetitions. A sample of about 500 songs was needed to include 97 percent of a male's repertoire.

Males delivered the various song types in sequences exhibiting marked stereotypy, some types having transition probabilities of 1.0 even when all subjects were taken into account. The greater the distance between territories of recorded males, the less similarity existed between their song-type sequences.

Evidence showed that neighbors matched song types when countersinging, although I could not determine the extent to which this occurred. Subjects of playback experiments eventually began to sing in response to the tape, and they were entrained to their position in the stereotyped sequence of song type delivery. Instead of copying the song type just played by the tape recorder, subjects often anticipated what the recorder would play next and sang that song type in advance of the recorder. Six subjects exhibited the extreme of such anticipation by correctly singing in advance of the recorder nine consecutive song types ($P = 114^{-9}$).

Differences between audible components of consecutive song types were determined for 15 parameters and compared with differences between the same parameters in a randomly generated sequence of the same song types. Only two of the 15 parameters exhibited significantly greater differences between successive songs in the real sequence when compared with the random sequence. I also found significant audible contrasts within song types.

I interpreted the results within the framework of Hartshorne's (1956) anti-monotony hypothesis, which was not so strongly supported by this study as originally expected. Instead, the results indicate that a combination of (1) variety of song output and (2) matching of song types in the structured countersinging of neighbors function together to preclude habituation effects postulated by Hartshorne.

Results support the views of Thielcke (1969) and Kroodsma (1974) that dialects are maintained because males learn their songs (in the case of marsh wrens, their song-type sequences) after they have dispersed from parental territories to more distant localities in which they eventually breed.

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